VEGETATION PATTERNS AND PLANT REPRODUCTIVE PROCESSES IN THE SUCCULENT KAROO

Karen Joan Esler

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SUMMARY

This thesis focuses on vegetation patterns and plant reproductive processes at the Tierberg Karoo Research Centre (33°10'S, 22°17'E) in the semi-arid southern Succulent Karoo, South Africa.

It begins with an investigation into the roles of soil properties and competition in explaining variation in species distributions. The aim was to investigate changes in soil properties associated with species turnover (replacement series). Patterns of species abundances have been attributed to cyclic succession driven by disturbance and inter-specific competition. Areas where dominant species replaced each other over apparent edaphic discontinuities were investigated to test the roles of soil properties and competition in explaining variation in species distributions. Only soil pH differed significantly across the gradients studied. However, inter- and intra-specific competitive interactions were also inferred. It was concluded that species distribution patterns resulted from the combined effects of edaphic factors and competition.

The bulk of the thesis focuses on the reproductive biology of key species in the cyclic succession in order to understand the demographic processes underlying these patterns. The vegetation model proposes that *heuweltjies* (or mima-like mounds) are the source of disturbance which initiates the successional process. A study of reproductive attributes of dominant species occurring on and off *heuweltjies* indicated that species occurring on *heuweltjies* had opportunistic life-history traits; seeds did not germinate readily and canopy seed banks were maintained. Species off *heuweltjies* had higher overall germination and did not maintain seed banks in the plant canopies. The differences in reproductive attributes were related to competition and disturbance.

The Mesembryanthema (in the family Aizoaceae) were the focus of the study because the ecology of this group is poorly understood. Members of this group are also keystone species in the successional pathway. A detailed study was

conducted on the seed biology of three Mesembryanthema species which play different roles in the dynamics of the study site. Variation in capsule and seed numbers were recorded over three different seed production events. Canopy-stored seed banks were not characteristic of the species studied. The seed source for species in favourable recruitment years is likely to be from seeds produced in the previous season. The reproductive biology of the study species reflected differences in the degree to which seeds banks were part of their strategy for survival in the successional framework.

In a general study of soil seed banks (in sites located off *heuweltjies*), seed bank densities were found to be low and distinctly seasonal (71-426 seeds per m^2 in summer versus 17-90 seeds per m^2 in winter), indicating the transient nature of most seeds in the seed bank. Seeds were not uniformly distributed and were more abundant under shrubs than in open areas. Seed abundance patterns were largely a result of dispersal differences among individual species. Soil seed densities did not correlate well with adult plant densities; species which were over-represented in the seed bank were identified as early successional in the vegetation dynamics model.

Field seedling recruitment was monitored at the same time as the seed banks were studied. The timing and amount of rainfall and the frequency of follow-up rains influenced germination response as well as seedling survival. Climate patterns at Tierberg are complex, but significant rainfall events are more predictable in April when recruitment events were recorded. Few seedlings survived, highlighting the slow population turnover. The patterns of seedling distributions could be explained in terms of the vegetation dynamics, although seedling survival did not differ among microhabitats. This challenges the view in the succession model that seedling recruitment of some species is facilitated by the presence of others. The dispersal characteristics of individual species may be more important. Seedlings found in supposedly more favourable microhabitats may not be "nursed" but, rather, "trapped". However in an experiment in which seedlings of three species were exposed to water stress, differences in the relative water stress tolerances

of the seedlings were demonstrated. Seedlings of species that were most abundant in sheltered habitats (under mature plant canopies) in the field were less tolerant to water stress than those which occurred in open habitats.

The thesis contributes to the understanding of karoo vegetation dynamics and is the first comprehensive study of seed and seedling biology in the Karoo. It also provides detailed information on the field ecology of the Mesembryanthema, an exceptionally speciose yet poorly understood taxon in the Karoo.

PREFACE

This thesis comprises papers to be submitted for publication (Chapters 3, 5 and 6); submitted for publication (Chapters 2 and 7) or published (Chapter 4, Appendix 1). I have presented the papers in a logical sequence as chapters, although this does not correspond with the sequence in which the papers were prepared. Appendix 1 is a paper in which I am second author; I was involved in all stages of the preparation of this paper. This paper provides an introduction to the plant species that occur on the study site as well as a model of the dynamics of the system, and should be read first. I refer to this paper as Yeaton and Esler (1990) in the text of the thesis. Most of the chapters in the thesis address questions which stemmed from Yeaton and Esler (1990). Part of the original data collection for Chapter 4 was done by Philip Ivey and the published paper is co-authored with my supervisor, Richard Cowling and Philip Ivey. A fellow post-graduate student and close friend, Nikki Phillips, and I shared equally in the planning and data collection for Chapter 7, although I did the bulk of the writing for this chapter. We have submitted this as a co-authored paper, with me as first author. Apart from these three instances, the thesis is entirely my own work.

The introductions to each chapter contain the relevant literature reviews for each particular research facet. To avoid repetition, this is kept to a minimum in the general introduction. Because the chapters are treated as separate publications, there is some degree of overlap (for example, in the study site descriptions).

ACKNOWLEDGEMENTS

I could not have asked for a nicer supervisor than Professor Richard Cowling. He gave me constant academic and moral support throughout this study. I will always admire his ability to instil enthusiasm in his students, his wonderful sense of humour, his generosity and most of all his fairness. It was a pleasure to be one of his students.

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Dick Yeaton was a key player in this thesis, and I thank him for the multitude of ways in which he helped. I was privileged to have the opportunity to work with Dick Yeaton on the paper in Appendix 1 and will always be grateful for his generous input into the thesis in general. Thank you to my parents, Bill and Gill Esler and to my dear friend Clare Griffiths for always being there.

I am very grateful to Philip Maund for assisting in the final preparation of this thesis.

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Chapter 7: Mr. F. Petrie, Dr. J.M. Van Heerden and the staff of the Elsenberg Agricultural College for their assistance and permission to carry out this study at Elsenberg; Bruce Bayer and Timm Hoffman for useful discussions; Willie Stock, Guy Midgely and Chris Stokes for commenting on earlier drafts.

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CONTENTS

CHAPTER 1

GENERAL INTRODUCTION

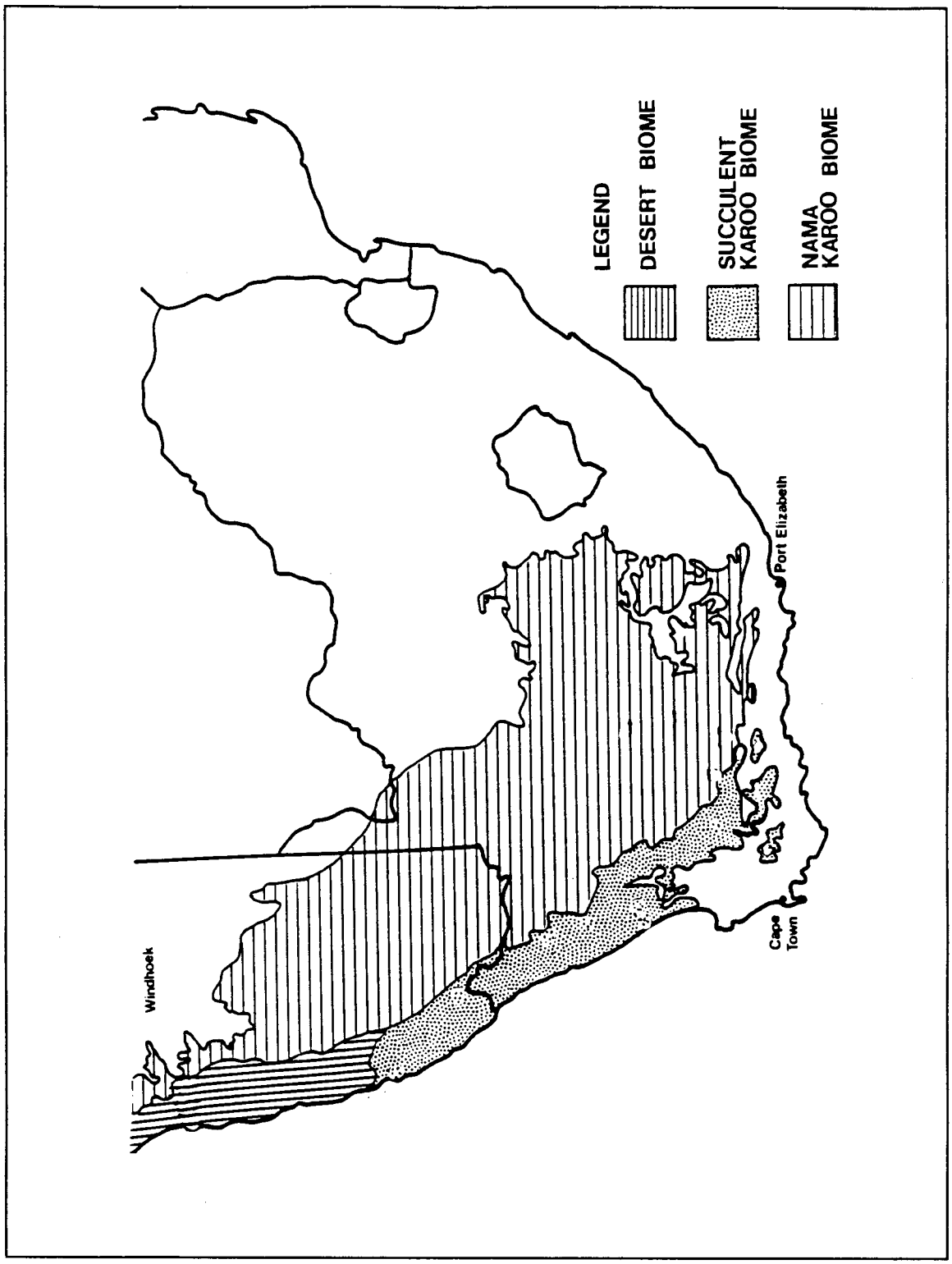
1.1 THE KAROO

The semi-arid and arid rangelands of South Africa are extensive, covering approximately 33% (427 000 km^2) of the land surface (Cowling 1986). The rangelands have been divided into three distinct biomes based on climatic variables and life form spectra; namely the Desert, Nama Karoo and Succulent Karoo biomes (Rutherford and Westfall 1986)(Fig. 1-1). This thesis focuses on the vegetation patterns and plant reproductive processes in the Succulent Karoo.

The Succulent Karoo biome occupies 4.3% of South Africa's land surface (Huntley 1984, Rutherford and Westfall 1986). It is a very species-rich region with high levels of diversity at all scales (Cowling et al. 1989). At the 1 000 m^2 scale, up to 113 species have been recorded, with a mean of 74 species. Such numbers are unparalleled for semi-arid shrublands (Cowling et al. 1989). The high levels of species diversity and endemism (Cowling et al. 1989) in the Succulent Karoo biome can be attributed to a relatively few number of families, one notably being the family Aizoaceae (other notable families include the Crassulaceae, Euphorbiaceae and Asclepiadaceae). The monophyletic, and entirely succulent Mesembryanthema group (sub-families Ruschioideae and Mesembryanthemoideae) within the Aizoaceae is remarkably speciose (ca. 2 000 spp.; Hartmann 1991) (Plate 1-2)(It must be noted that the term Mesembryanthema is used to ease communication, but it has no taxonomic basis). The Succulent Karoo biome largely derives its name from this group. Like most succulents, the Mesembryanthema are tolerant of drought, but require predictable rainfall in order to persist (Von Willert et al. 1985). Thus, the Succulent Karoo biome is largely confined to areas which receive low, but predictable (mostly winter), rainfall (Jürgens 1986, Hilton-Taylor and Le Roux 1989, Hartmann 1991, Cowling et al. submit.). There have been very few ecological studies conducted on the Mesembryanthema, which is surprising since this group is such an important component of the Succulent Karoo.

The vegetation of the Succulent Karoo is a dwarf succulent shrubland (Acocks 1953, Cowling 1986, Hoffman and Cowling 1987). The prominent growth forms

Figure 1-1. The semi-arid and arid rangelands of southern Africa (from Cowling et al. submit.).



are the similar dwarf and low leaf succulents, although stem succulents and deciduous and evergreen dwarf shrubs are also common (Cowling et al. submit.). Most semi-arid and arid regions comprise two distinct groups of plants: the long-lived perennials which tolerate drought, and the short-lived annuals which evade drought (Noy-Meir 1985, Shmida et al. 1986). The Succulent Karoo is interesting in that an additional group of short- to medium-lived (ca. 2-10 years) shrubs are abundant, mostly belonging to the Mesembryanthema. In the area in which this study was conducted, these short- to medium-lived shrubs dominate *heuweltjies* or mima-like mounds (Lovegrove and Siegfried 1986) (Plate 1-3). Disturbance levels are higher on *heuweltjies*, which support a different biota and soil chemistry from their adjacent surroundings (Midgely and Musil 1990). There is a close relationship between the incidence of *heuweltjies* and the distribution of succulent karoo vegetation. It is believed that termites are responsible for the creation of *heuweltjies* (Milton and Dean 1990).

1.2 THESIS RATIONALE

Over the last three centuries, the diverse flora of the Karoo has reportedly undergone wide scale and dramatic change (Acocks 1953). This is a source of great concern amongst farmers who have witnessed a decline in palatable plant production and to conservationists who are concerned about threats to biotic diversity (Hilton-Taylor and Le Roux 1989). The advent of pastoralism and the small stock industry has been widely cited as the main cause of vegetation change in the Karoo (Acocks 1953, Roux and Vorster 1983). The small stock industry, however, generates more than 20% of the total gross value of South African livestock products (Burger 1991), and contributes significantly to the national income (Roux et al. 1981, Vorster and Roux 1983). South Africa's gross domestic product is influenced by karoo vegetation as a source of fodder (Burger 1991). The karoo vegetation is a resource that will continue to be exploited.

The balance between the maintenance of ecological processes in the Karoo and

continued livestock production has to be based on a sound understanding of the ecological processes which govern vegetation change. It was with this realisation that the Karoo Biome Programme was initiated in 1986 (Cowling 1986). Ecological studies in the Karoo were largely descriptive until the start of the Karoo Biome Project, which was coordinated and funded by the Foundation for Research Development of the Council for Scientific and Industrial Research (Cowling 1986). The programme initiated a surge of scientific interest in the area which hitherto had received little attention. The areas of research which required specific attention were those involving an understanding of the dynamic relationships between species and of the processes which determined these relationships. This thesis, which was initiated as part of the Karoo Biome Project, represents a first attempt to do both.

The management of any system is based on an understanding of its dynamics. The current rangeland management policies in the Karoo are centred on the notion that communities develop in predictable steps until a dynamic equilibrium or "climax" is reached (Teague 1987, Hoffman and Cowling 1987). This climax is supposedly determined by climate, and if undisturbed, is stable. Grazing is seen as an agent of disturbance which alters this predictable, deterministic developmental sequence. These ideas have been criticised by southern African ecologists who argue that predictable series of species replacements are not possible in systems whose dynamics are governed by spatially and temporally variable climatic sequences (Hoffman and Cowling 1987, Mentis et al. 1989). The problem is that little factual basis for either concept of vegetation dynamics existed until recently. Yeaton and Esler (1990, see Appendix 1) provide inferential evidence that succession does occur in the southern Succulent Karoo. This successional process does not incorporate the "climax" concept, but rather, is based on the concept of cyclic succession. *Heuweltjies* are seen a source of disturbance in the succession, and the processes which govern the changes can largely be explained in terms of plant reproductive biology, although the edaphic environment may also play a role in determining vegetation patterns (Fig. 1-2).

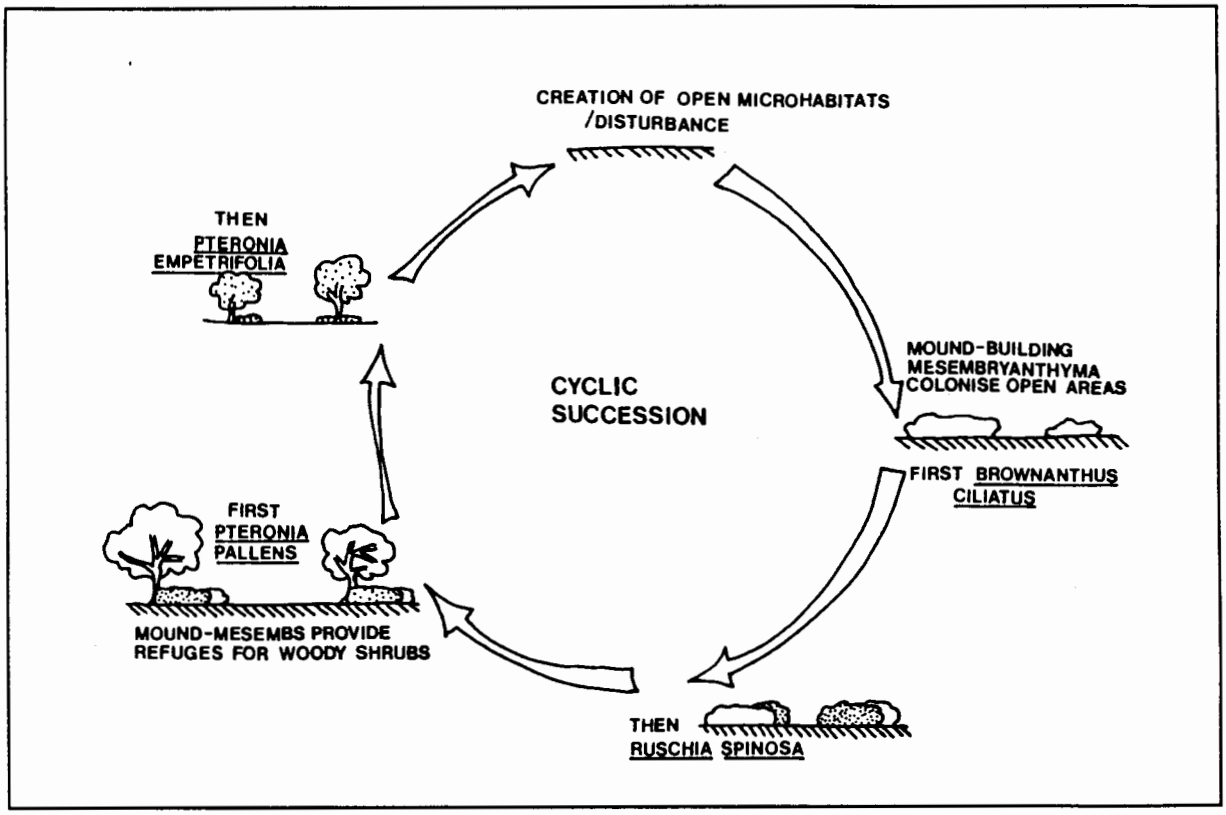


Figure 1-2. Diagrammatic representation of the cyclic succession model (Yeaton and Esler 1990).

This thesis represents a study of the processes which underlie or govern these changes. The thesis has three main objectives:

1. To fill a gap in terms of the knowledge of the reproductive biology of karoo plants.

Information on seed production, seed banks, seed germination and seedling recruitment is generally lacking in the Karoo. There have been a few studies on the germination of karoo shrubs (Henrici 1935, 1939) and on seed banks of annuals (Van Rooyen and Grobbelaar 1982), but this thesis represents one of the first comprehensive works on reproductive biology in karoo vegetation. Seed banks and seedling establishment were studied over two years and emphasis was placed on the importance of the microhabitat. This detailed investigation into spatial and temporal patterns at the regeneration phase is seen as a major strength of the thesis.

2. To focus on the reproductive biology of key species in the cyclic succession in order to understand the demographic processes underlying these successional patterns.

An attempt is made to provide an understanding of the dynamics of this system as described in a model of the vegetation dynamics (Yeaton and Esler 1990). Some of the demographic predictions of this model (Fig. 1-2) are tested by studying the reproductive processes at the community, population and individual levels. An hierarchical approach was adopted in order to exploit the significance of the findings in the thesis at different levels of organisation.

3. To focus on the Mesembryanthema (family Aizoaceae) since the ecology of this group is poorly understood.

Although the thesis does not deal exclusively with the Mesembryanthema, an attempt was made to focus on this group where possible. Members of this taxon are keystone species in the successional pathway (Yeaton and Esler 1990). Most of the work on the Mesembryanthema has been done at a systematic (Hartmann 1991) and a biogeographic (Jürgens 1986) level. Apart from a few studies on pollination ecology (Guess and Guess 1989, Struck 1990) and dispersal ecology (Garside and Lockyer 1930, Lockyer 1932, Ihlenveldt 1971, Van Rooyen et al. 1980), very little is known about the reproductive ecology of this group. In a recent review of the Mesembryanthema (Hartmann 1991), only six (5.9%) of the 102 papers quoted on this group had a reproductive ecology theme.

1.3 STUDY SITE

Field work was conducted at the Tierberg Karoo Research Centre (33°10'S, 22°17'E) which is situated on the southern edge of the Great Karoo, 25 km east of Prince Albert, Cape Province, South Africa (Fig. 1-3). The study area is situated on a colluvial plain (800 m altitude) in the Sand river valley which lies between two ridges, the Tierberg ridge (1 200 m) to the north, and the Droëkloofberg (1 291 m) to the south. These ridges are composed of Ecca shales, Dwyka tillites and Witteberg quartzites (Milton et al. 1992). The site is 20 km north of the Swartberg

Mountains, a range of the Cape Folded Belt, which run parallel to the Indian Ocean, some 100 km to the south.

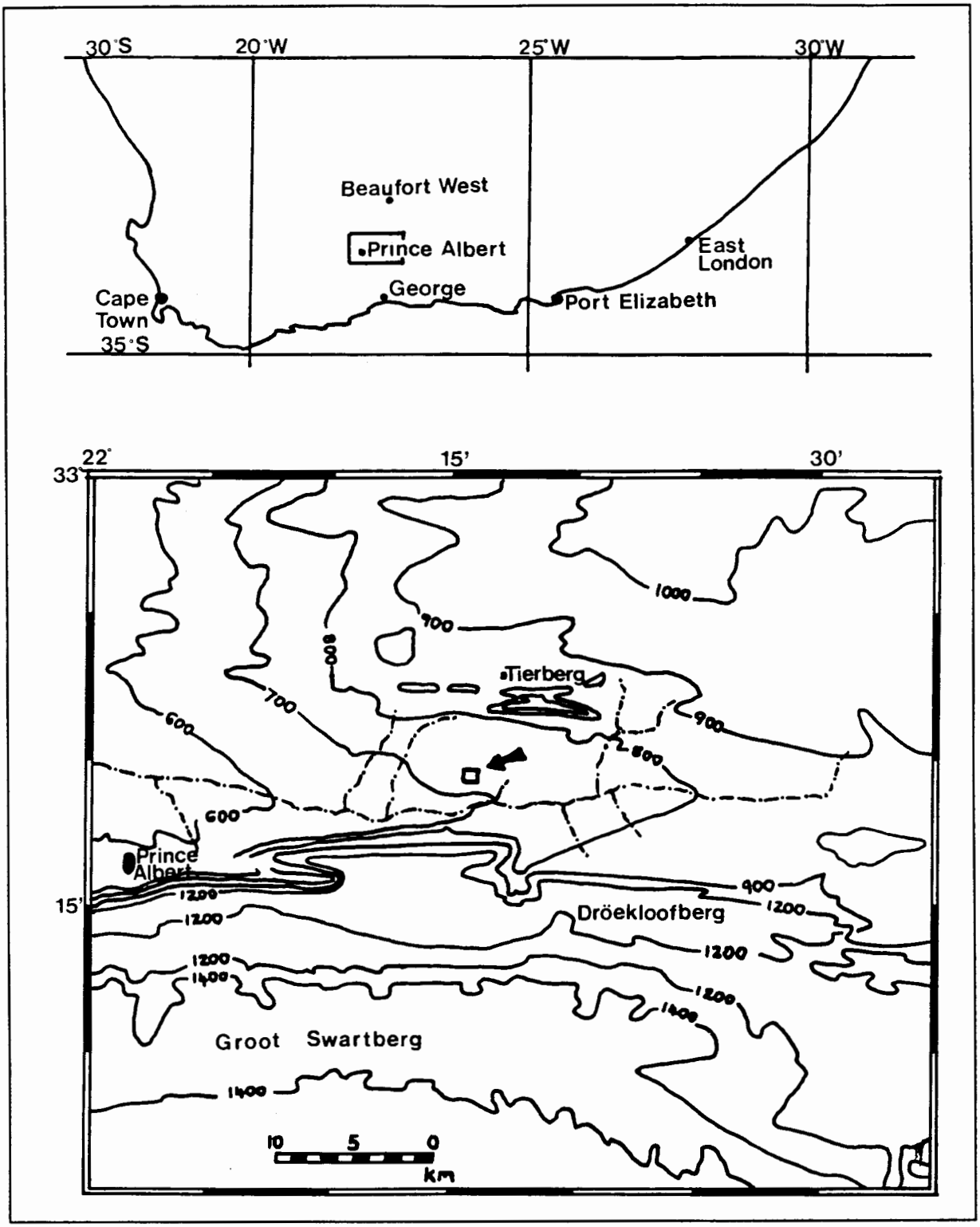


Figure 1-3. Location of the study site (the Tierberg Karoo Research Centre) in relation to the coast, mountain ranges, major rivers and towns (adapted from Milton et al. 1992).

The study site has generally weakly structured soils which are very deep (> 2 m) sandy loams. The soils of the A horizon have a variable nutrient status, but are generally alkaline with relatively high levels of phosphorus and potassium. *Heuweltjies*, which occur at a density of 2.05 ± 0.13 per ha^{-1}, are higher in organic matter, nutrients and salt concentrations (Milton et al. 1992).

The climate is influenced by circumpolar westerly cyclonic fronts and alternating high pressure cells. The former are more frequent during winter (associated with north-westerly winds) whereas the latter are more common in summer (associated with south-easterly winds) (Fig. 1-4).

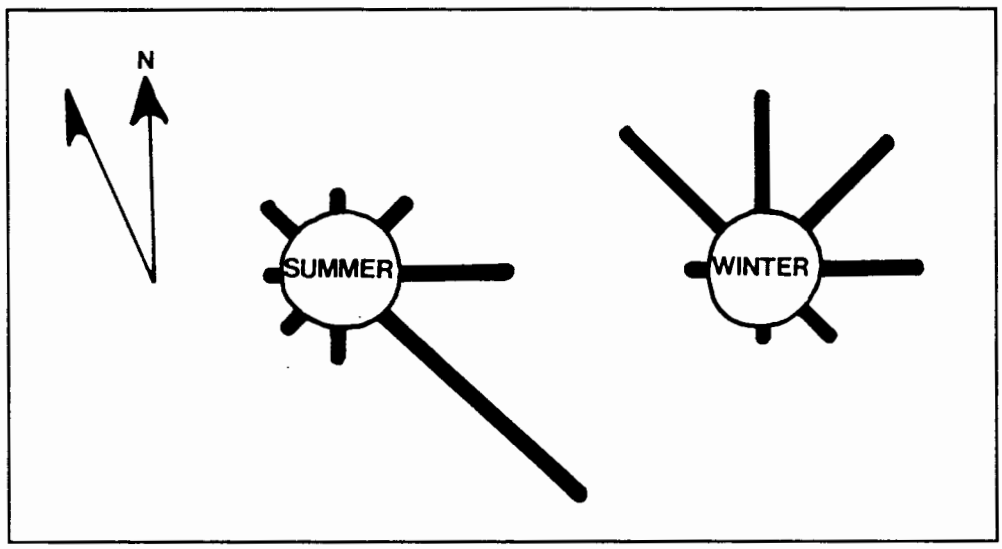


Figure 1-4. Wind roses showing wind directions at the Tierberg Karoo Research Centre in summer and winter (from Milton et al. 1992).

Rainfall (Schulze and McGee 1978, Venter et al. 1986) is associated with:

1. The westerly cyclonic fronts in winter. The associated moisture bands must be deep enough to penetrate the Cape fold mountains. The ensuing rainfall is usually not heavy and events seldom exceed more than 10 mm.
2. The moist air advected from high pressure cells in the southwestern Indian Ocean. The associated rain occurs mainly in spring and summer and is not reliable (again, because of the fold mountains).
3. The cut-off low pressure systems which have their highest frequencies at the equinoxes in spring and autumn. Moist air is drawn in from the north (Congo air)

and from the Indian Ocean by these cut-off lows which are responsible for substantial but infrequent rainfall events.

4. The intrusion of moist, unstable tropical air from the north. This causes thunderstorms which occur in late summer/autumn (February to April).

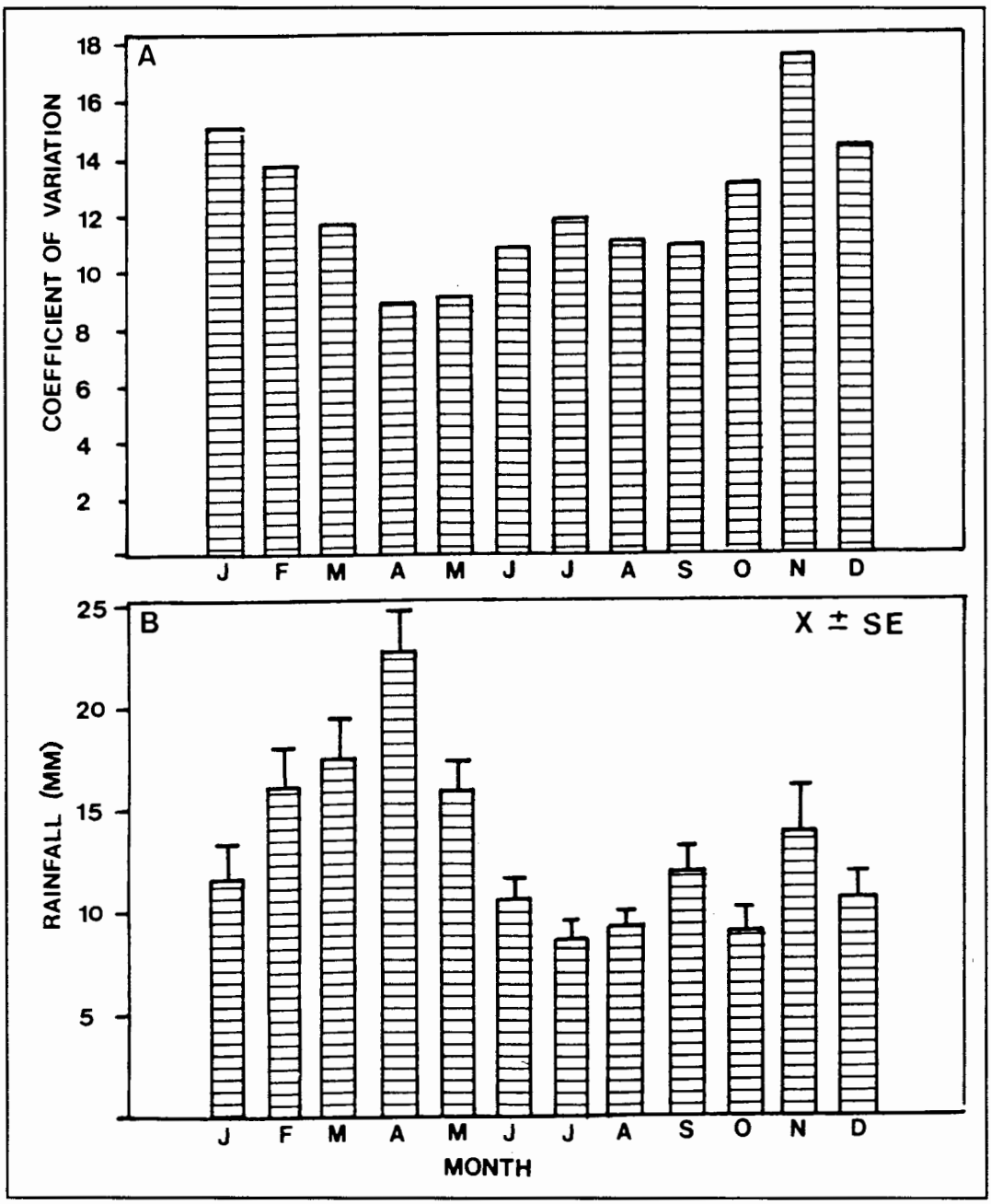


Figure 1-5. a) Monthly coefficients of variation in rainfall and b) mean monthly rainfall generated for a site 14 km from Tierberg. Data for 100 years were obtained from the rainfall simulation programme GENRAIN (Zucchini and Adamson 1984). This programme uses rainfall records from existing weather stations to generate artificial rainfall sequences. The closest weather station to the study site was Zachariasfontein, 14 km northwest of Tierberg (33°5'S, 22°0'E).

The study site receives approximately 170 mm of rain per year from these different sources. During the data collection period of this study (1986-1990), annual rainfall was generally higher than the mean annual rainfall, except for 1987. The rainfall totals for 1986 to 1990 were 204.9 mm, 134.3 mm, 297.0 mm, 245.5 mm and 193.0 mm respectively (Milton et al. 1992). In order to obtain long sequences of precipitation data which were not available for the study site, a rainfall simulation computer programme, GENRAIN (Zucchini and Adamson 1984) was used to generate artificial rainfall sequences from which coefficients of variation for yearly rainfall (n = 100 years) and for monthly rainfall were calculated (Fig. 1-5). The simulated data showed that most of the rain falls in autumn (March to May) and to a lesser extent in spring (September to November) (Fig. 1-5). Rainfall is highest in autumn because it is derived from three sources in these months. In winter and summer, rain is low and unpredictable since it is derived from only one source in both of these seasons. The coefficient of variation for yearly rainfall was 37.75 (mean rainfall = 161.12 mm; standard deviation = 60.82). This is low indicating that the site has a relatively reliable annual rainfall, certainly compared with many other Succulent and Nama Karoo sites (Fig. 1-6). The lowest monthly coefficient of variation in rainfall was recorded in April (Fig. 1-5a). This month also had the highest mean monthly rainfall (Fig. 1-5b). April and May have the highest frequency of rainfall events greater than 10 mm (Fig. 1-7). Temperatures at the study site range from -5°C in winter to 43°C in summer, with a mean annual temperature of 17.5°C (Milton et al. 1992) (Fig. 1-8).

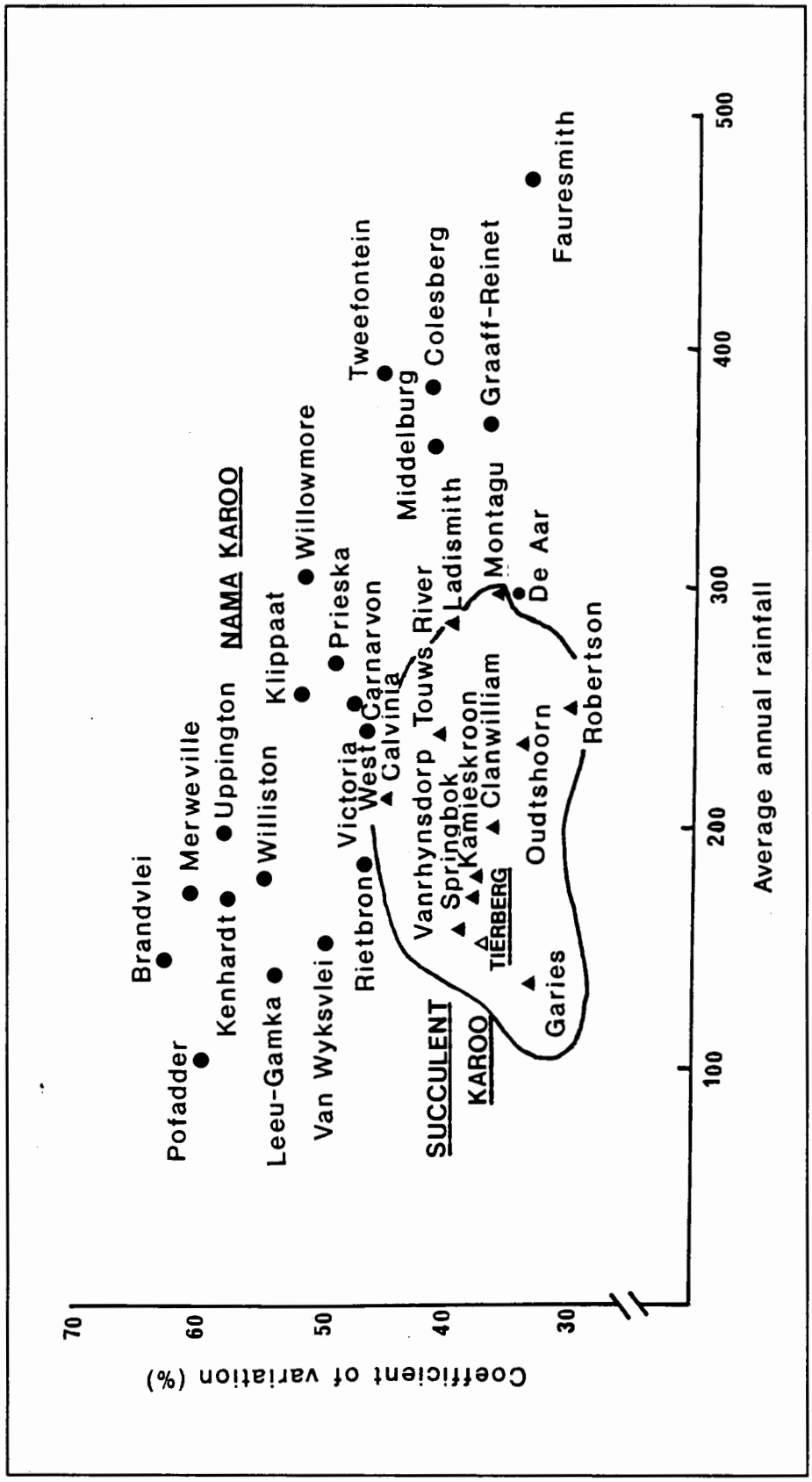


Figure 1-6. Average annual rainfall versus coefficient of variation for 31 sites in the Karoo. Except for Tierberg, data are from Hoffman and Cowling (1987).

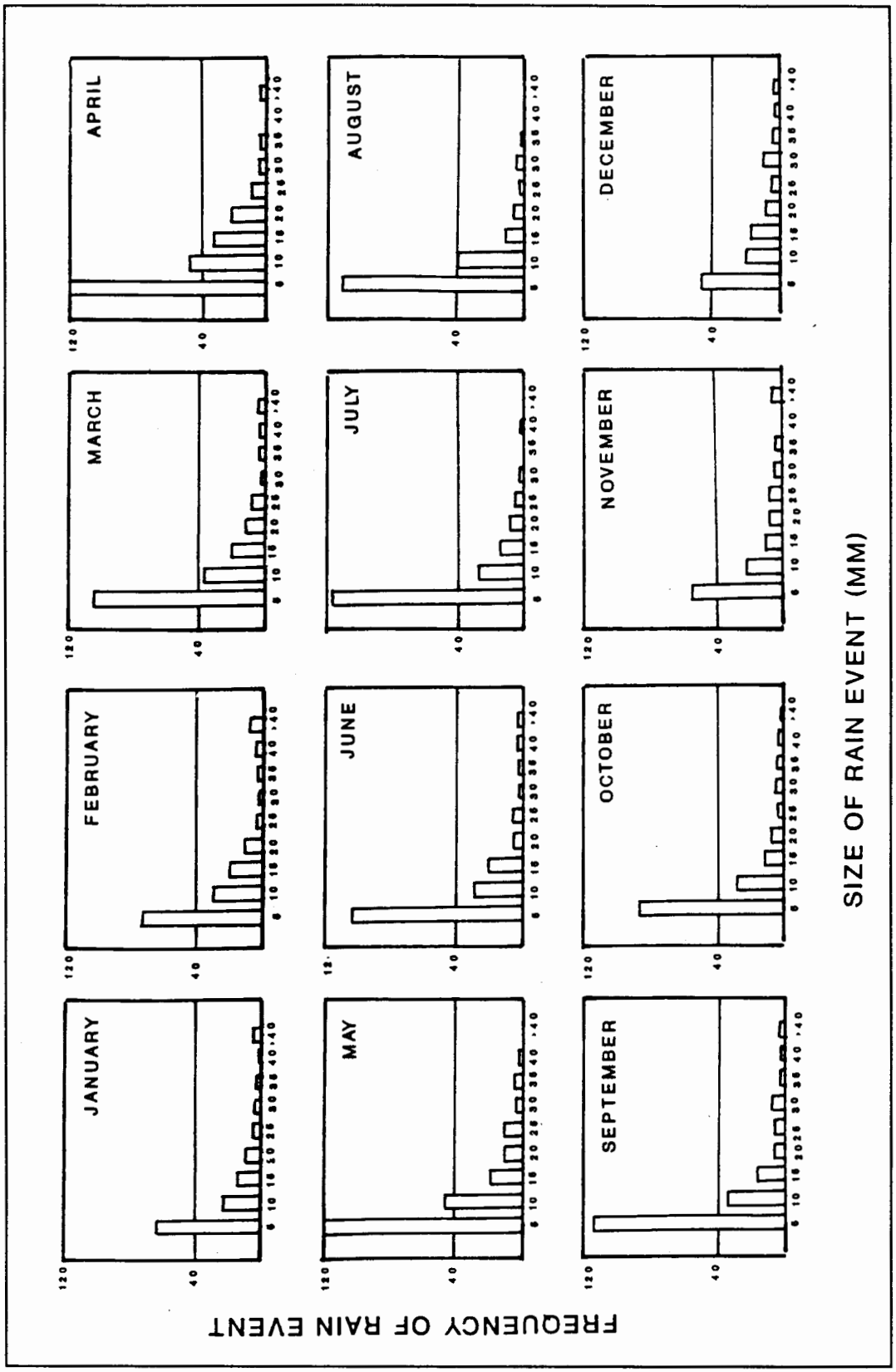


Figure 1-7. Frequencies of rainfall events of different sizes from January to December. Data for 100 years were obtained from the rainfall simulation programme GENRAIN (Zucchini and Adamson 1984).

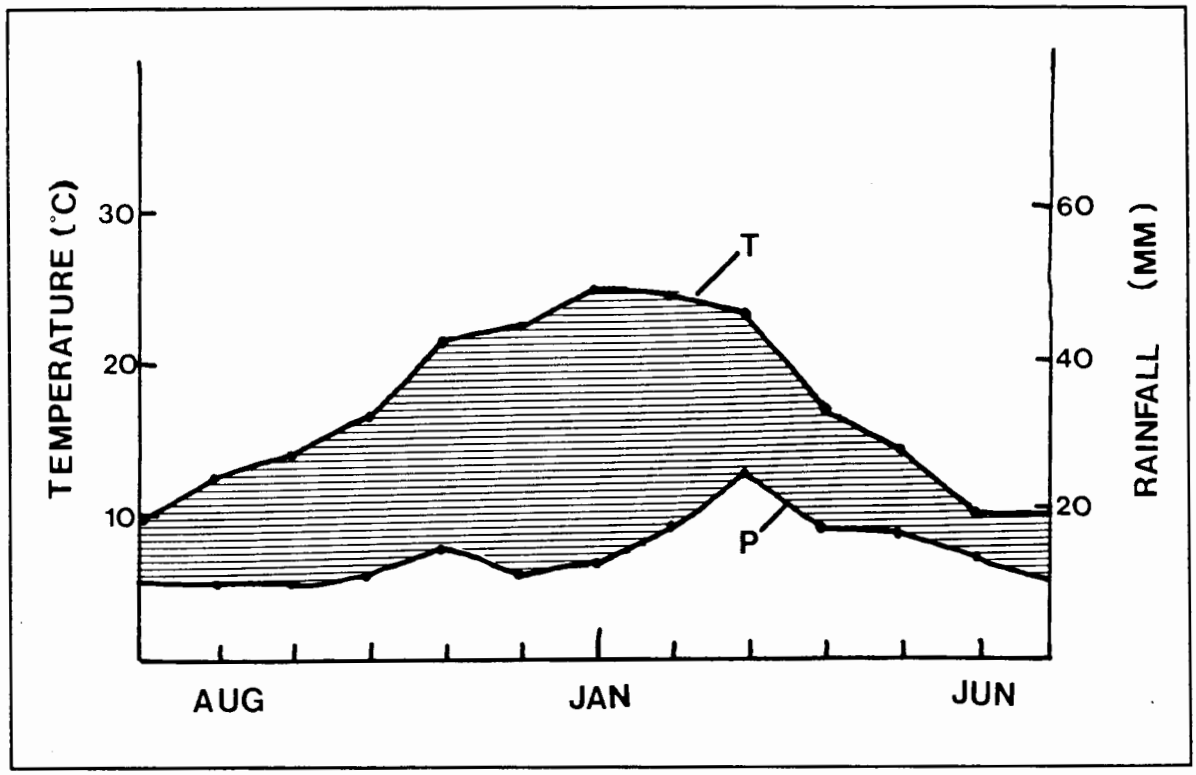


Figure 1-8. Walter Leith climate diagram for the Tierberg Karoo Research Centre. Temperature data are from the Tierberg study site (September 1987 to January 1990) and rainfall data are from the Prince Albert gaol (92 years, from 1895 to 1987). P = mean monthly rainfall in mm; T = mean monthly temperature in degrees centigrade (from Milton et al. 1992).

Milton et al. (1992) recognised four types of habitats on the study site; the "flats" (or plains), *heuweltjies*, and minor and major drainage lines. The first two habitats form the primary focus of this thesis. The vegetation on the flats (70% of the area) is relatively homogeneous, comprising perennial succulent (predominantly Mesembryanthema spp.) and non-succulent shrubs (Asteraceous spp. e.g. Pteronia). The predominance of succulents and the distinct lack of grasses indicates that the vegetation is part of the Succulent Karoo biome (Rutherford and Westfall 1986, Cowling et al. submit.). However, geographically the site is marginal to the Succulent Karoo biome since it borders on the Great Karoo, characterised by grassy dwarf shrublands typical of the Nama Karoo biome. *Heuweltjies* (3% of the area) are nutrient rich, circular soil mounds which are probably derived from termite activity (Milton and Dean 1990). They support a set

of plant species distinct from the surrounding vegetation in areas (like the study site) which have not been heavily utilised by domestic stock (Chapter 3). However, in disturbed sites which have been heavily exploited by domestic stock, species which are normally associated with *heuweltjies* also occur on the flats.

The study area, now protected from domestic herbivory but lightly grazed by wild herbivores (20 ha per Small Animal Unit (SAU)), was previously (before June 1987) moderately grazed (60 ha SAU^{-1} or 8 kg ha^{-1}) (Milton et al. 1992).

Because each chapter is written as a separate paper, a description of the study site, along with details relevant to that chapter is provided; thus, there is some degree of overlap with this section.

1.4 THESIS STRUCTURE AND OUTLINE

The study begins with Appendix 1 (Yeaton and Esler 1990) which comprises an investigation into the pattern and process of succulent karoo vegetation. This paper focuses on the biotic controls of community structure. Patterns of relative abundance and distribution of species at the Tierberg study site were used to indicate species associations. For those species with inferred positive associations, nearest-neighbour analysis was employed as a measure of competitive interaction. A working model of the dynamics of the system was developed. This model implies that the structure and dynamics of the system revolves around a predictable sequence of species replacements, driven primarily by biotic interactions (Fig. 1-2, Plate 1-6). The chapters in this thesis test various hypotheses which were generated from this paper. It must be noted that Eberlanzia cf. vulnerans, the mat-forming species of Mesembryanthema referred to in Yeaton and Esler (1990) (formerly in the family Mesembryanthemaceae, now in the family Aizoaceae) is now known as Ruschia spinosa (L.) H.E.K. Hartm. & Stuber. Two forms of this species occur on the study site. These have also been called Eberlanzia cf. macroura (L.Bol.) L.Bol. (tall growth form) and Eberlanzia cf.

vulnerans (L.Bol.) L.Bol. (short mat-forming growth form) in some publications (Milton et al. 1992). These are now considered to be different growth forms of the same species referred to as Ruschia spinosa in this thesis (Plates 1-5 and 1-6).

In Chapter 2, the roles of soil properties and competition in explaining variation in species distributions were investigated. In the Prince Albert region of the Succulent Karoo, some species appear to replace each other over apparent edaphic discontinuities. It was suggested in Yeaton and Esler (1990) that biotic interactions strongly influence the structure of these communities. This contrasts with the idea that habitat specialisation is a mechanism which structures plant communities. Chapter 2 investigates these mechanisms in more detail. Chapter 3 deals with a different source of pattern in the Succulent Karoo, associated with *heuweltjies* (Plate 1-3). This is a study of the reproductive biology of species that occur on and off *heuweltjies*, which are highlighted as important in the model discussed in Yeaton and Esler (1990). Chapters 4, 5 and 6 deal with pattern and process at a population and community level. They address predictions deduced from the successional model, and comprise an investigation into seed production of selected species as well as seed bank dynamics (Plates 1-4 and 1-5), and field seedling establishment. The primary focus of these studies is the role of the microhabitat in determining successful recruitment and establishment of karoo plant species. Chapter 7 is an investigation of seedling survivorship of selected species in an experimental environment and attempts to relate this to the field situation. Finally, in Chapter 8, major findings from the study are summarised along with recommendations for future research.

Plate 1-1. The study site looking north towards the Tierberg range. The prominent growth forms are (1) the dwarf, evergreen leaf-succulents (the arrow indicates a mat-forming species of Mesembryanthema, Brownanthus ciliatus) and (2) low, evergreen and semi-deciduous shrubs (the arrow indicates Pteronia pallens). This photograph was taken in spring during the peak flowering period.

Plate 1-2. The hygrochastic capsules diagnostic of the Mesembryanthema (Family Aizoaceae). These open during rain when moisture conditions are more favourable for germination and establishment (Chapter 4).

Plate 1-3. Vegetation on *heuweltjies* is distinct from the surrounding flats vegetation (dotted lines indicate the boundary of the *heuweltjie*). Species occurring on *heuweltjies* are mainly short to medium lived evergreen leaf succulents. This photograph was taken in mid-summer; note that many of the flats species are semi-deciduous (cf. plate 1-1) (Chapter 3).

Plate 1-4. In the seed bank study, soil cores were collected from the Tierberg Karoo Research Centre and were placed in seed trays at the Worcester Botanical Gardens (33°36'S, 19°27'E) where they were monitored over the entire seasonal range. This photograph shows the experimental set-up at Worcester (Chapter 5).

Plate 1-5. Seed decay was measured by placing seed bags into the field and by recording remaining viable seeds over two years. This seed bag was placed under the canopy of a mat-forming species of Mesembryanthema, Ruschia spinosa (Chapter 5).

Plate 1-6. The vegetation model proposed by Yeaton and Esler (1990, Appendix 1) attributes patterns of species abundance in the Karoo to cyclic succession driven by disturbance and inter-specific competition. Brownanthus ciliatus (1) is a primary coloniser in the successional sequence. In time, this species is replaced by Ruschia spinosa (2) and a woody shrub guild (Appendix 1).

1.5 REFERENCES

Acocks,J.P.H. 1953. Veld types of South Africa. Memoirs of the Botanical Survey of South Africa 28:1-128.

Burger,J.D. 1991. An economic overview of Karoo utilisation in relation to the national situation. Unpublished paper presented at the 1991 Arid Zone Ecology Forum annual research meeting, South Africa.

Cowling,R.M. 1986. A description of the Karoo Biome Project. South African National Scientific Programmes Report No. 122, Council for Scientific and Industrial Research, Pretoria. 42pp.

Cowling, R.M., Gibbs Russell,G.E., Hoffman,M.T. and Hilton-Taylor,C. 1989. Patterns of plant species diversity in southern Africa. In: Biotic diversity in southern Africa: concepts and conservation, ed. B.J. Huntley, Oxford University Press, Cape Town. pp 19-50.

Cowling,R.M., Esler,K.J., Midgely,G.F. and Honig,M.A. Submit. Plant functional diversity, species diversity and climate in arid and semi-arid southern Africa. Journal of Arid Environments.

Garside,S. and Lockyer,S. 1930. Seed dispersal from the hygroscopic fruits of Mesembryanthemum carpanthea (Mesembryanthemum), pomeridiana N.E. Br. Annals of Botany 44:639-655.

Guess,S.K. and Guess,F.W. 1989. Flower visiting masarid wasps in southern Africa (Hymenoptera: Vespoidea: Masaridae). Annals of the Cape Provincial Museums, natural history 18:95-134.

Hartmann,H.E.K. 1991. Mesembryanthema. In: Systematics, biology and evolution of some South African taxa, eds. P. Goldblatt, H.E.K. Hartmann,

E.G.H. Oliver, H.P. Linder and B.E. Van Wyk, Contributions to the Bolus Herbarium 13:75-157.

Henrici,J.M. 1935. Germination of karoo bush seeds. South African Journal of Science 32:223-234.

Henrici,J.M. 1939. Germination of karoo bush seeds. South African Journal of Science 36:212-219.

Hilton-Taylor,C. and Le Roux,A. 1989. Conservation status of the Fynbos and Karoo biomes. In: Biotic diversity in southern Africa: concepts and conservation, ed. B.J. Huntley, Oxford University Press, Cape Town. pp 202-223.

Hoffman,M.T. and Cowling,R.M. 1987. Plant physiognomy, phenology and demography. In: The Karoo biome: a preliminary synthesis. Part 2. - vegetation and history, eds. R.M. Cowling and P.W. Roux. South African National Scientific Programmes Report No. 142, Council for Scientific and Industrial Research, Pretoria. pp 1-34.

Huntley,B.J. 1984. Characteristics of South African biomes. In: Ecological effects of fire in South African ecosystems, eds. V. Booysen and N.M. Tainton. Ecological Studies: Analysis and Synthesis Vol 48, Springer-Verlag, Berlin. pp 1-17.

Ihlenfeldt,H.D. 1971. Some aspects of the biology of dissemination of the Mesembryanthemaceae. In: The genera of the Mesembryanthemaceae, ed. H. Herre. Tafelberg, Cape Town. pp 28-34.

Jürgens,N. 1986. Contributions to the ecology of southern African succulent plants. Mitteilungen aus dem Institut für Allgemeine Botanik 21:139-365.

Lockyer,S. 1932. Seed dispersal from hygroscopic Mesembryanthemum fruits; Bergeranthus scapigerus Schw., and Dorotheanthus bellidiformis N.E. Br., with a note on Carpanthea pomeridiana N.E. Br. Annals of Botany 46:323-342.

Lovegrove,B.G. and Siegfried,W.R. 1986. Distribution and formation of mima-like earth mounds in the western Cape Province of South Africa. South African Journal of Science 82:432-436.

Mentis,M.T., Grossman,D., Hardy,M.B., O'Connor,T.G and O'Reagan,P.J. 1989. Paradigm shifts in South African range science management and administration. South African Journal of Science 85:684-687.

Midgely,G.F. and Musil,C.F. 1990. Substrate effects of zoogenic soil mounds on vegetation composition in the Worcester-Robertson valley, Cape Province. South African Journal of Botany 56:158-166.

Milton,S.J. and Dean,W.R.J. 1990. Mima-like mounds in the southern and western Cape: are the origins so mysterious? South African Journal of Science 86:231-233.

Milton,S.J., Dean,W.R.J. and Kerley,G.I.H. 1992. Tierberg Karoo Research Centre: history, physical environment, flora and fauna. Transactions of the Royal Society of South Africa 48:15-46.

Noy-Meir,I. 1985. Desert ecosystem structure and function. In: Hot deserts and arid shrublands vol. A., eds. M. Evenari, I. Noy-Meir, and D.W. Goodall. Elsevier, Amsterdam. pp 93-103.

Roux,P.W. and Vorster,M. 1983. Vegetation change in the Karoo. Proceedings of the Grassland Society of South Africa 18:25-29.

Roux,P.W., Vorster,M., Zeeman,P.J.L. and Wentzel,D. 1981. Stock production in the karoo region. Proceedings of the Grassland Society of South Africa 16:29-35.

Rutherford,M.C. and Westfall,R.H. 1986. The biomes of southern Africa - an objective categorisation. Memoirs of the Botanical Survey of South Africa 54:1-98.

Schulze, R.E. and McGee,O.S. 1978. Climatic indices and classification in relation to the biogeography of southern Africa. In: Biogeography and ecology of southern Africa, ed. M.J.A. Werger. Junk, The Hague. pp 19-54.

Shmida,A., Evenari,M. and Noy-Meir,I. 1986. Hot desert ecosystems. An integrated view. In: Hot deserts and arid shrublands vol B., eds. M. Evenari, I. Noy-Meir, and D.W. Goodall. Elsevier, Amsterdam. pp 379-387.

Struck,M. 1990. Contributions to the phenology and anthecology of permanent plots in the arid winter rainfall region of southern Africa (German). Philosophy of Science Thesis. Department of Biology, University of Hamburg. 80pp.

Teague,W.R. 1987. Plant growth and response to defoliation. In: Veld management in the eastern Cape, eds. J.E. Danckwerts and W.R. Teague. Pasture Research, Stutterheim. 337pp.

Van Rooyen,M.W., Barkhuizen,A. and Myburgh,S.E. 1980. Saadverspreiding van enkele verteenwoordigers van die Mesembryanthemaceae. South African Journal of Botany 46: 173-192.

Van Rooyen,M.W. and Grobbelaar,N. 1982. Saadbevolkings in die grond van die Hester Malan-natuurreservaat in die Namakwalandse Gebrokeveld. South African Journal of Botany 1:41-50.

Venter,J.M., Mocke,C. and De Jager,J.M. 1986. Climate. In: Part 1 - physical environment, eds. R.M. Cowling and P.W. Roux. South African National Scientific Programmes Report No 124, Council for Scientific and Industrial Research, Pretoria. pp 39-51.

Von Willert,D.J., Brinckmann,E., Scheitler,B. and Eller,B.M. 1985. Availability of water controls crassulacean acid metabolism in succulents of the Richtersveld (Namib desert, South Africa). Planta 164:45-55.

Vorster,M. and Roux,P.W. 1983. Veld of the karoo areas. Proceedings of the Grassland Society of Southern Africa 18:18-24.

Yeaton,R.I. and Esler,K.J. 1990. The dynamics of a succulent karoo vegetation: a study of species association and recruitment. Vegetatio 88:103-113.

Zucchini,W. and Adamson,P. 1984. The occurrence and severity of droughts in South Africa. Water Research Commission report No. 91/1/84, Department of Civil Engineering, University of Stellenbosch. 191pp.

CHAPTER 2

EDAPHIC FACTORS AND COMPETITION AS DETERMINANTS OF PATTERN IN SOUTH AFRICAN KAROO VEGETATION

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2.1 ABSTRACT

The roles of edaphic factors and competition in explaining species distribution of Pteronia (Family Asteraceae) dominated plant communities were investigated. Soil characteristics, species plant covers and competitive interactions were determined at three sites (one on a colluvial plain and two on tillite slopes) on the farm Tierberg in the semi-arid Karoo, South Africa. These sites represented areas where Pteronia species replace each other over apparently distinct habitats. Direct (Canonical Correspondence Analysis, CCA) and indirect (Detrended Correspondence Analysis, DCA) gradient analyses gave similar eigenvalues, indicating that edaphic variables accounted for much of the variation in species data. The first axis of the CCA-biplot separated species on the colluvial plain from those on tillite slopes along a soil texture gradient. The separation of species in the second CCA axis indicated that soil phosphorous, pH, magnesium and calcium levels were also important in determining species distribution patterns. Together these axes accounted for 50.1% of the variation in the species data. Nearest-neighbour analyses indicated that there were strong inter- and intra-specific competitive interactions at Pteronia community boundaries. It was concluded that Pteronia species distribution patterns in the Karoo result from the combined effects of soil physico-chemical factors and competition.

2.2 INTRODUCTION

For semi-arid regions, the Succulent Karoo biome of southern Africa (Rutherford and Westfall 1986) is unusually rich in plant species both at a local and a regional scale (Cowling et al. 1989). Many of these species belong to a few prominent families, notably Aizoaceae, Crassulaceae and Asteraceae. Even within these families, a few large genera contribute notably to species diversity. Sixty out of a total of seventy five species in the genus Pteronia (Asteraceae) occur in the semi-arid regions of southern Africa (C. Hilton-Taylor, unpublished data, Department of Botany, University of Cape Town). High species turnover along environmental gradients (beta diversity) is recorded for Succulent Karoo communities (Jürgens 1986, Cowling et al. 1989). Turnover is often abrupt resulting in narrow boundaries between communities (Lloyd 1989a,b, Smitheman and Perry 1990, Yeaton and Esler 1990).

Only recently have attempts been made to understand the role played by biotic and abiotic factors in determining Karoo community structure and composition (Yeaton and Esler 1990). The slow rate of population change in these systems, and the difficulties involved in doing field manipulations make field experiments difficult. As an alternative, pattern analysis can provide inferred descriptions of the dynamics of these systems. These techniques are extremely valuable since they allow the formulation of a variety of hypotheses on species interactions and more generally, on the underlying causes of species coexistence and diversity (Fonteyn and Mahall 1981, Cody 1986a,b, Yeaton and Esler 1990).

In the Prince Albert region of the Succulent Karoo, there are many cases of Pteronia species replacing each other over apparent edaphic discontinuities. In this chapter, the roles of soil properties and competition in explaining the variation in species distributions were investigated.

The following questions were addressed:

(1) What is the relationship between soil factors and community composition in the southern Succulent Karoo?

There are many studies in arid and semi-arid regions which have found strong vegetation-soil relationships at a variety of scales (e.g. Stein and Ludwig 1979, Olsvig-Whittaker et al. 1983, Key et al. 1984, Wierenga et al. 1987, Olsvig-Whittaker 1988). In southern African semi-arid systems, soils have been shown to play a role in determining transitions between vegetation types (Palmer et al. 1988, Palmer 1991a,b) as well as between different plant communities or assemblages (Snijman and Perry 1987, Lloyd 1989a,b, Smitheman and Perry 1990). Most of the latter studies have been phytosociological in nature, dealing with a large number of communities and species. These have made qualitative assessments of soil-vegetation relationships. More quantitative studies are needed. Midgely and Musil (1990) provide quantitative data of soils on and off *heuweltjies* (or mima-like mounds, Lovegrove and Siegfried 1986) and the associated species changes. In this case, edaphic specialisation was clearly demonstrated.

(2) What evidence is there for biotic interactions across species boundaries?

The importance of competition as a force structuring karoo plant communities was addressed in Yeaton and Esler (1990). In this chapter, the patterns of abundance and distribution among and within karoo plant species at Tierberg in the Succulent Karoo were discussed. It was suggested that biotic interactions strongly influence the structure of karoo plant communities. One possibility is that if community boundaries are determined mainly by competition, strong competitive interactions would occur at the species interfaces. Alternatively, if patterns were the result of edaphic specialisation, one would expect competitive interactions to be weaker at the species interfaces (since each species would be physiologically adapted to exploit resources differentially, thus minimising niche overlap). In this case, intra-specific competition should be stronger than inter-specific competition. Unfortunately, this view is simplistic, since if patterns were determined to some extent by edaphic specialisation, one could also expect competitive interactions to be strong at the species interfaces due to asymmetrical competition (i.e. where

soils are slightly in favour of one, that species is strongly more competitive, and vice versa). The point is, that it is not possible to establish the exact roles of competition and edaphic specialisation using pattern analysis alone. However, the advantage of this preliminary investigation is that directions for future research can be established.

2.3 METHODS

2.3.1 Study area and site location

Field work was conducted on the farm Tierberg, situated about 25 km east of Prince Albert, on the southern edge of the Great Karoo, Cape Province, South Africa (33°9'S, 22°16'E). The area receives approximately 170 mm of rain per year, falling mostly in autumn (March-May) and, to a lesser extent, spring (September-November). Temperatures range from -5°C (winter minimum) to 43°C (summer maximum), with a mean annual temperature of 17.5°C (Milton et al. 1992). The vegetation has a high proportion of succulent species and a low abundance of grasses, and resembles Acocks' (1975) Little Karoo form of Karroid Broken Veld (Milton et al. 1992).

Three sites were chosen within the study area. These all represented areas where Pteronia spp. replace one another (termed Pteronia replacement series) over apparently distinct habitats. The first study site, termed the F (flats) site was situated within the relatively flat, 100 ha Tierberg Karoo Research Centre (800 m altitude). The soils of this site are generally weakly structured and very deep (> 2 m) sandy loams of colluvial origin (Milton et al. 1992). Two Pteronia spp. occur in the flats site: P. pallens L.F. grows in lower lying regions and at the edges of drainage lines and washes, whilst P. cf. empetrifolia DC. is confined mainly to slightly higher lying areas (Milton et al. 1992). Rare species co-occurrences are mostly at the boundaries between these two habitats.

The second and third study sites were situated on a small ridge called Tierberg (altitude 840 m), located to the north at a distance of three km from the F site. These two sites (one km apart) occur on soils derived from the Dwyka tillite formation (Visser 1986) and were termed T1 (tillite 1) and T2 (tillite 2) respectively. P. pallens was a dominant species at the bottom of the T1 slope, whilst P. viscosa Thunb. occurred further up-slope. The two species coexisted over a narrow (10 m) boundary. In contrast, P. pallens occurred at the top of the T2 slope on soils derived from the Whitehill Formation, a bed of white weathering carbonaceous shale with chert (Visser 1986). Further down the slope, P. viscosa was dominant, once again on soils derived from tillite.

2.3.2 Sampling procedures

2.3.2.1 Vegetation

Transects, 100 m long, were located at each site. They were orientated to avoid *heuweltjies*, which are known to be edaphically distinct from surrounding vegetation (Midgely and Musil 1990), and were positioned across Pteronia replacement series. Three, 5 x 5 m quadrats were located in the middle and at the two ends of each transect. Quadrat positions represented areas where Pteronia species were dominant (or co-dominant) and interface regions where Pteronia species distributions overlapped. Within each quadrat, individual plants (of all species) were identified and counted. Their canopy diameters along two axes (L and W) at right angles to each other were measured. Plant species covers were calculated according to the formula: $\pi LW/4$.

Nearest-neighbour analysis (Pielou 1960, 1962) was used to determine if intraspecific and interspecific interactions were occurring between Pteronia species. At each site Pteronia individuals were randomly chosen along 1 m wide, line transects. Transects were positioned to avoid drainage lines and *heuweltjies*. Measurements of canopy diameters of Pteronia individuals and their nearest-neighbour Pteronia spp. were determined. The distances between shrub centres

were measured, and the identities of the two individuals were recorded. One hundred measurements were taken for each intra- and inter-specific nearest-neighbour pair.

2.3.2.2 Soils

In each quadrat, three soil-samples were taken to a depth of 10 cm from open areas between shrubs following the removal of surface litter. Open areas between shrubs were chosen, as plants are known to affect physical and chemical soil properties through alteration of infiltration and run-off (Rostagno et al. 1991). Soil samples from each quadrat were bulked, dried at 60°C to a constant mass, and sieved through a 2 mm mesh.

Estimates of the percentage soil surface area covered by rocks were made from measurements of rock diameters along randomly placed 1 m rules (five per quadrat). The length of the rule covered by rocks was translated into percentage rock cover. Soil water infiltration rates were measured according to the method of Dean (1992). In each quadrat, three open ended cylinders (diameter = 7 cm) were placed into the soil to approximate depths of 1 cm in open areas between shrubs. Care was taken not to disturb the soil surface. The time taken for 100 ml of water to penetrate the soil was recorded for each cylinder. Soil depth was recorded in open areas by hammering a thin metal stake into the soil until bed-rock was reached. For the T1 and T2 sites, this method was relatively accurate, since the soil profiles were shallow. For the flats site however, this method was unsatisfactory, since the soils, of colluvial origin, were much deeper (over 2 m).

2.3.3 Data and statistical analyses

Seventeen soil-physical and chemical properties of the A-horizon (on average the top 10 cm layer of soil) were analysed: pH (in 1m KCl), resistance, leachable phosphorus, potassium, sodium, calcium, magnesium, copper, zinc, manganese, boron ($\mu g\ g^{-1}$), % total nitrogen and % silt, clay, medium, coarse and fine sand.

Soil analyses were conducted by the Department of Agriculture, Winter Rainfall Region, Elsenberg.

Single factor Analysis of Variance tests (ANOVAs) were used to test for significant differences in measured soil physico-chemical properties (pH and % data were normalised using an arcsin transformation), nearest-neighbour distances and Pteronia canopy areas along the Pteronia replacement series on tillite slopes and on the flats. Significantly different means were separated using Tukey multiple range tests (Zar 1984).

Species cover data and soil data were ordinated using both indirect (Detrended Correspondence Analysis) and direct (Canonical Correspondence Analysis) gradient analysis techniques (Ter Braak 1986, 1987a,b,c). In Detrended Correspondence Analysis (DCA)(Hill and Gauch 1980), axes are 'extracted' from the species data alone. Environmental gradient interpretations then follow. These are obtained using correlations of soil factors on the site scores of the DCA axes. In Canonical Correspondence Analysis (CCA), axes are selected as linear combinations of known environmental variables (Ter Braak 1986, 1987a,b). Species are plotted on the axes according to their optimal abundances and sites are plotted as weighted averages of their component species. CCA is designed to detect patterns of variation in species data that are best explained by the measured environmental variables. The end product is an ordination diagram that expresses not only variation in species distributions, but also the main relationships between environmental variables and species. For both techniques, eigenvalues indicate the importance of an axis, and species-environment correlation coefficients indicate the correlation between site scores which are linear combinations of environmental variables (Ter Braak 1986). Interset correlations are the coefficients of correlations between environmental variables and species axes based on the site scores (Ter Braak 1987a). A useful approach is to use DCA and CCA together to see how much of the variation in the species data is accounted for by the environmental data (Ter Braak 1986). Where the solutions for these analyses do not differ greatly, one can infer that the environmental variables measured account for much

of the variation in species data (Ter Braak 1986).

On an initial CCA run, high variance inflation factors indicated multicollinearity (Ter Braak 1987a) and prompted the removal of the following variables from the analysis: % silt, medium and fine sand. No weighting or detrending was applied. The 14 variables used in the CCA and DCA analyses are presented in Table 2-3. A Monte-Carlo permutation test was used to test the significance of the eigenvalues of the first canonical axis of the CCA ordinations (Ter Braak 1987a).

Inter- and intra-specific interactions were analysed using the nearest-neighbour analysis technique (Pielou 1960, 1962). The distances between Pteronia individuals were regressed against the sum of their covers for each intra- and inter-specific case. A significant positive relationship between these parameters indicates that a competitive interaction may be occurring, since the distance at which two individuals establish limits the size to which they grow.

2.4 RESULTS

Species richness and community composition along Pteronia replacement series differed on both tillite slopes and flats. The tillite slope quadrats dominated by Pteronia pallens tended to have fewer species than those dominated by P. viscosa (Fig. 2-1). On the flats site (F) this trend was not observed. In general, more species were recorded on the tillite sites (T1 and T2) than the F site (Fig. 2-1). In all transects, individuals of P. pallens were more frequent and had higher cover values than either P. viscosa or P. empetrifolia individuals (Appendix 2.8).

An analysis of the soil data alone indicated that only soil pH differed significantly across the Pteronia replacement series on both tillite slopes and flats (Table 2-1). Sites dominated by P. Pallens always had soils with a higher pH (Table 2-1). There was a great deal of variation in the nutrient status of the soils sampled, however increases in soil pH were accompanied by substantial increases in soil phosphorus,

and to a lesser extent, soil nitrogen levels (Table 2-1). Sites dominated by P. pallens tended to have higher nutrient levels than sites dominated by either P. viscosa or P. empetrifolia. In general, soils from the F site were lower in nutrients and pH than those on tillite slopes (Table 2-1). Soil depth at the F site was greater than that at the tillite sites. A soil pit dug at the F site (in an area dominated by P. pallens) indicated a soil depth of at least 2m. Soils at the tillite sites were more shallow (< 100 mm).

The ordinations by DCA and CCA produced similar eigenvalues for the first axes, but for the other three axes, eigenvalues of the DCA were substantially lower (Table 2-2). Species-environment correlation coefficients were marginally higher for the CCA axes (Table 2-2). This is expected since the CCA axes are based on species scores coupled with environmental variables.

The first two axes of the CCA bi-plot on the entire adjusted data set (27 quadrats, 14 variables) accounted for 50.1% of the variance in the species data (Fig. 2-2, Table 2-2). A Monte-Carlo permutation test (Ter Braak 1987a) showed that the first canonical axis was highly significant ($P < 0.01$) indicating that variation in species abundances was related to variation in environmental factors. On this axis, tillite slopes were separated from the flats site along a strong soil texture and chemical gradient. The most important soil parameters were % coarse sand, % nitrogen, resistance and pH (Fig. 2-2). The different Pteronia associations separated out along the second ordination axis and were best correlated with soil phosphorus, pH, calcium and magnesium (Fig. 2-2, Table 2-3). Areas dominated by P. pallens had soils with mostly higher elemental concentrations and more alkaline soils (Fig. 2-2). There was little separation of species associations on T1 and T2 tillite slopes which indicated a similarity in general species composition on both slopes.

Regression analyses for all intra- and inter-specific nearest-neighbour pairs of Pteronia on the tillite slopes yielded significant linear relationships (Fig. 2-3). The following regressions for intra- and inter-specific interactions on the flats were

obtained from Yeaton and Esler (1990): P. pallens-P. pallens: $Y = 69.0x + 350.9$, $r^2 = 0.69$, $P < 0.01$; P. empetrifolia-P. empetrifolia: $Y = 35.0x + 403.3$, $r^2 = 0.46$, $P < 0.01$; P. pallens-P. empetrifolia: $Y = 29.0x + 622.1$, $r^2 = 0.27$, $P < 0.01$. On the tillite transects, mean distances between intra-specific pairs were greater than the mean distances between inter-specific species pairs (Table 2-4). Individuals growing at the boundaries between species distributions (i.e. individuals measured as inter-specific pairs) tended to be smaller (Table 2-5). Correlation coefficients for the tillite slopes indicated that the strongest competitive relationships were between P. pallens-P. pallens pairs (r for T1 = 0.73, T2 = 0.66) and P. pallens-P. viscosa pairs (r for T1 = 0.71, T2 = 0.66) and that the weakest relationships were between P. viscosa-P. viscosa pairs (r for T1 = 0.28, T2 = 0.46).

Table 2-1. Soil physical and chemical data from Pteronia replacement series along three transects (tillite 1, tillite 2 and flats) at Tierberg in the Karoo. Data are means ± standard errors from three 5 x 5 m^2 quadrats sampled at three localities along each transect. Soil variables are abbreviated as follows (excluding standard abbreviations): res = resistance, %N = % total Nitrogen, depth = soil depth (mm). Infiltration is measured in minutes and seconds. One way analysis of variance was conducted on soil variables at each locality within a transect. Significant differences between localities (ANOVA) are indicated as follows: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$. Where a Tukey multiple range analysis ($P < 0.05$) indicated significant differences within sites, the symbols a, b and c are used.

Tillite 1				
	P. viscosa	boundary	P. pallens	Sig.
pH	5.97 ± 0.33^{a}	6.23 ± 0.15^{ab}	6.6 ± 0.10^{c}	*
res	2106.7 ± 393.33	1566.67 ± 218.58	1520.00 ± 248.46	N.S.
%N	5.97 ± 0.03	6.23 ± 0.15	6.6 ± 0.1	N.S.
P($\mu g\ g^{-1}$)	64.33 ± 5.49	93.67 ± 13.70	111.67 ± 17.29	N.S.
K($\mu g\ g^{-1}$)	126.00 ± 9.02	145.67 ± 24.01	148.67 ± 12.55	N.S.
Na($\mu g\ g^{-1}$)	63.67 ± 3.84	67.67 ± 9.39	71.67 ± 7.88	N.S.
Ca($\mu g\ g^{-1}$)	2.55 ± 0.09^{a}	4.17 ± 0.56^{b}	4.92 ± 0.12^{b}	**
Mg($\mu g\ g^{-1}$)	1.50 ± 0.04^{a}	2.04 ± 0.25^{b}	2.02 ± 0.01^{b}	***
Cu($\mu g\ g^{-1}$)	0.87 ± 0.06^{a}	1.29 ± 0.06^{a}	0.97 ± 0.02^{b}	***
Zn($\mu g\ g^{-1}$)	1.17 ± 0.06	1.06 ± 0.03	0.98 ± 0.08	N.S.
Mn($\mu g\ g^{-1}$)	79.00 ± 5.58^{a}	148.35 ± 3.83^{b}	110.79 ± 3.57^{c}	***
B($\mu g\ g^{-1}$)	0.17 ± 0.01	0.32 ± 0.61	0.25 ± 0.02	N.S.
%silt	8.00 ± 1.15	11.33 ± 1.33	8.67 ± 0.67	N.S.
%clay	6.00 ± 0.00	10.67 ± 1.76	8.00 ± 1.15	N.S.
%coarse sand	29.47 ± 3.7	25.85 ± 1.17	27.62 ± 2.24	N.S.
%medium sand	19.41 ± 1.65	17.83 ± 1.30	16.37 ± 1.83	N.S.
%fine sand	36.91 ± 1.02	34.32 ± 1.61	39.35 ± 1.48	N.S.
%rock	33.80 ± 1.32^{a}	33.80 ± 1.64^{a}	16.00 ± 4.45^{b}	*
infiltration	2:00 ± 0:37	3:52 ± 2:03	4:36 ± 1:17	N.S.
depth(mm)	80.55 ± 6.96	80.00 ± 15.84	76.66 ± 11.67	N.S.
Tillite 2				
	P. viscosa	boundary	P. pallens	Sig.
pH	6.20 ± 0.35^{a}	7.20 ± 0.30^{ab}	7.90 ± 0.06^{b}	*
res	1673.33 ± 221.01	1373.33 ± 40.55	1046.67 ± 224.00	N.S.
%N	6.20 ± 0.35^{a}	7.20 ± 0.30^{b}	7.90 ± 0.06^{b}	**
P($\mu g\ g^{-1}$)	136.33 ± 36.61^{a}	172.00 ± 18.72^{ab}	278.67 ± 18.68^{b}	*

Table 2-1 (continued).

K(μg g^{-1})	177.00 ± 40.00^{a}	229.00 ± 43.47^{ab}	546.00 ± 121.70^{b}	*
Na(μg g^{-1})	70.67 ± 9.02	55.33 ± 2.33	202.00 ± 113.16	N.S.
Ca(μg g^{-1})	6.98 ± 2.82	11.73 ± 0.65	19.30 ± 0.86	N.S.
Mg(μg g^{-1})	1.57 ± 0.16	2.13 ± 0.45	5.14 ± 1.91	N.S.
Cu(μg g^{-1})	1.77 ± 0.31	2.47 ± 0.09	2.72 ± 0.34	N.S.
Zn(μg g^{-1})	1.76 ± 0.24^{a}	2.07 ± 0.11^{a}	3.05 ± 0.25^{b}	*
Mn(μg g^{-1})	286.18 ± 103.41	441.11 ± 43.64	259.33 ± 112.06	N.S.
B(μg g^{-1})	0.32 ± 0.07	0.40 ± 0.09	0.54 ± 0.13	N.S.
%silt	12.00 ± 0.00^{a}	10.00 ± 0.00^{b}	15.33 ± 0.67^{c}	***
%clay	9.33 ± 1.76	10.00 ± 1.15	14.00 ± 2.00	N.S.
%coarse sand	30.34 ± 1.28^{a}	33.92 ± 4.75^{ab}	20.74 ± 1.20^{b}	*
%medium sand	18.53 ± 1.02^{a}	16.11 ± 1.31^{ab}	13.32 ± 0.81^{b}	*
%fine sand	29.79 ± 2.00	29.98 ± 3.37	36.61 ± 1.47	N.S.
%rock	29.80 ± 5.49	28.73 ± 2.39	33.60 ± 3.29	N.S.
infiltration	3:16 ± 1:00	6:71 ± 0:53	6:58 ± 1:23	N.S.
depth(mm)	63.33 ± 13.02	40.56 ± 0.55	46.33 ± 10.59	N.S.
Flats				
	P. empetrifolia	**boundary**	**P. pallens**	**Sig.**
pH	4.83 ± 0.18^{a}	5.20 ± 0.51^{a}	6.73 ± 0.09^{b}	*
res	1173.33 ± 426.67	570.00 ± 65.06	903.33 ± 178.36	N.S.
%N	4.83 ± 0.17	5.20 ± 0.51	6.73 ± 0.09	N.S.
P(μg g^{-1})	47.33 ± 4.67	57.67 ± 2.19	216.67 ± 76.5	N.S.
K(μg g^{-1})	98.67 ± 2.91^{a}	116.00 ± 18.04^{a}	117.67 ± 6.39^{b}	*
Na(μg g^{-1})	236.67 ± 63.00	125.00 ± 14.57	110.00 ± 17.06	N.S.
Ca(μg g^{-1})	3.38 ± 0.24^{a}	3.32 ± 0.34^{a}	8.38 ± 1.85^{b}	*
Mg(μg g^{-1})	2.60 ± 0.29^{a}	2.39 ± 0.29^{a}	4.21 ± 0.37^{b}	*
Cu(μg g^{-1})	0.82 ± 0.02	0.99 ± 0.19	1.22 ± 0.07	N.S.
Zn(μg g^{-1})	0.84 ± 0.07	2.25 ± 1.35	1.40 ± 0.17	N.S.
Mn(μg g^{-1})	74.19 ± 23.91^{a}	135.62 ± 26.01^{ab}	188.65 ± 6.12^{b}	*
B(μg g^{-1})	0.40 ± 0.08	0.35 ± 0.10	0.40 ± 0.12	N.S.
%silt	6.00 ± 0.00	12.67 ± 2.91	16.00 ± 3.06	N.S.
%clay	24.00 ± 4.00^{a}	10.00 ± 3.06^{a}	8.67 ± 0.67^{b}	*
%coarse sand	41.37 ± 4.66	43.49 ± 1.72	43.29 ± 4.10	N.S.
%medium sand	13.19 ± 0.72	14.42 ± 0.68	16.86 ± 1.63	N.S.
%fine sand	15.51 ± 1.17	19.42 ± 1.75	15.19 ± 4.03	N.S.
%rock	2.47 ± 1.24	3.80 ± 0.81	1.73 ± 0.58	N.S.
infiltration	9:18 ± 1:02	10:03 ± 2:01	7:77 ± 0:76	N.S.
depth(mm)	>1000	>1000	>1000	-

Table 2-2. Comparison of the results of Detrended Correspondence analysis (DCA) and Canonical Correspondence analysis (CCA) of the entire data set (81 species in 27 sites), a) eigenvalues and b) species-environment correlation coefficients for the four species ordination axes, and c) percentage of variance (cumulative) accounted for in the species-environment relationships.

Axis	1	2	3	4
a) eigenvalues				
DCA	0.879	0.245	0.138	0.068
CCA	0.807	0.583	0.397	0.224
b) species-environment correlation coefficients				
DCA	0.942	0.735	0.880	0.858
CCA	0.964	0.986	0.890	0.898
c) % variance (cumulative)				
DCA	27.6	32.3	0	0
CCA	29.1	50.1	64.5	72.5

Table 2-3. Canonical correspondence analysis (CCA) of the full data set (27 quadrats and 14 soil variables) from the three transects (tillite 1, tillite 2 and flats) at Tierberg in the Karoo. Inter-set correlations of environmental variables for all four axes. This CCA is illustrated in Fig. 2-1.

	Inter-set correlations			
Axis	**1**	**2**	**3**	**4**
Ph	-0.488	0.687	0.121	0.285
Resistance	-0.536	-0.138	-0.383	-0.234
Phosphorus	-0.132	0.737	0.097	0.269
Potassium	-0.375	0.437	0.402	0.210
Sodium	0.265	-0.129	0.435	-0.035
Calcium	-0.307	0.554	0.342	0.408
Magnesium	0.230	0.529	0.325	0.058
Copper	-0.469	0.316	0.206	0.521
Zinc	-0.085	0.086	0.319	0.220
Manganese	-0.285	0.185	-0.093	0.643
Boron	0.115	0.114	0.378	0.446
% Clay	0.281	-0.336	0.533	0.168
% Coarse sand	0.808	-0.175	-0.143	0.135
% Nitrogen	-0.580	-0.144	-0.439	0.491

Table 2-4. Nearest neighbour distances for Pteronia pallens (Pp) and P. viscosa (Pv) inter- and intra-specific pairs from two transects (tillite 1 and tillite 2) at Tierberg in the Karoo. Data are means ± standard errors, n = 100. One way analysis of variance was conducted on data from three localities within each transect (*** = $P < 0.001$). Similar superscripts indicate means that are not significantly different (Tukey multiple range analysis; $P < 0.05$).

	Nearest-neighbour distances				
Species pairs	**Pp/Pp**	**Pv/Pv**	**Pp/Pv**	**F-ratio**	**Sig.**
tillite 1	88.55 ± 3.26[a]	86.50 ± 2.98[a]	66.35 ± 3.73[b]	13.52	***
tillite 2	80.40 ± 3.04[a]	81.60 ± 3.02[a]	58.70 ± 2.71[b]	19.37	***

Table 2-5. Canopy areas (cm^2) of Pteronia pallens (Pp) and Pteronia viscosa (Pv) individuals when interacting as inter- (n = 100) and intra-specific (n = 200) pairs. Data (means ± standard errors) are from two transects (tillite 1 and tillite 2) on the farm Tierberg in the Karoo. T-tests indicate significant differences (*** = $P < 0.001$) between sizes of plants growing with individuals of the same and different species.

	Canopy Areas			
	Pp with Pp	**Pp with Pv**	**t**	**Sig.**
tillite 1	2837.87 ± 146.20	1967.80 ± 148.47	3.75	***
tillite 2	2798.03 ± 124.23	1497.98 ± 158.04	6.99	***
	Pv with Pv	**Pv with Pp**	**t**	**Sig.**
tillite 1	1416.34 ± 60.22	1086.05 ± 66.88	3.39	***
tillite 2	1580.40 ± 72.67	950.24 ± 122.92	4.97	***

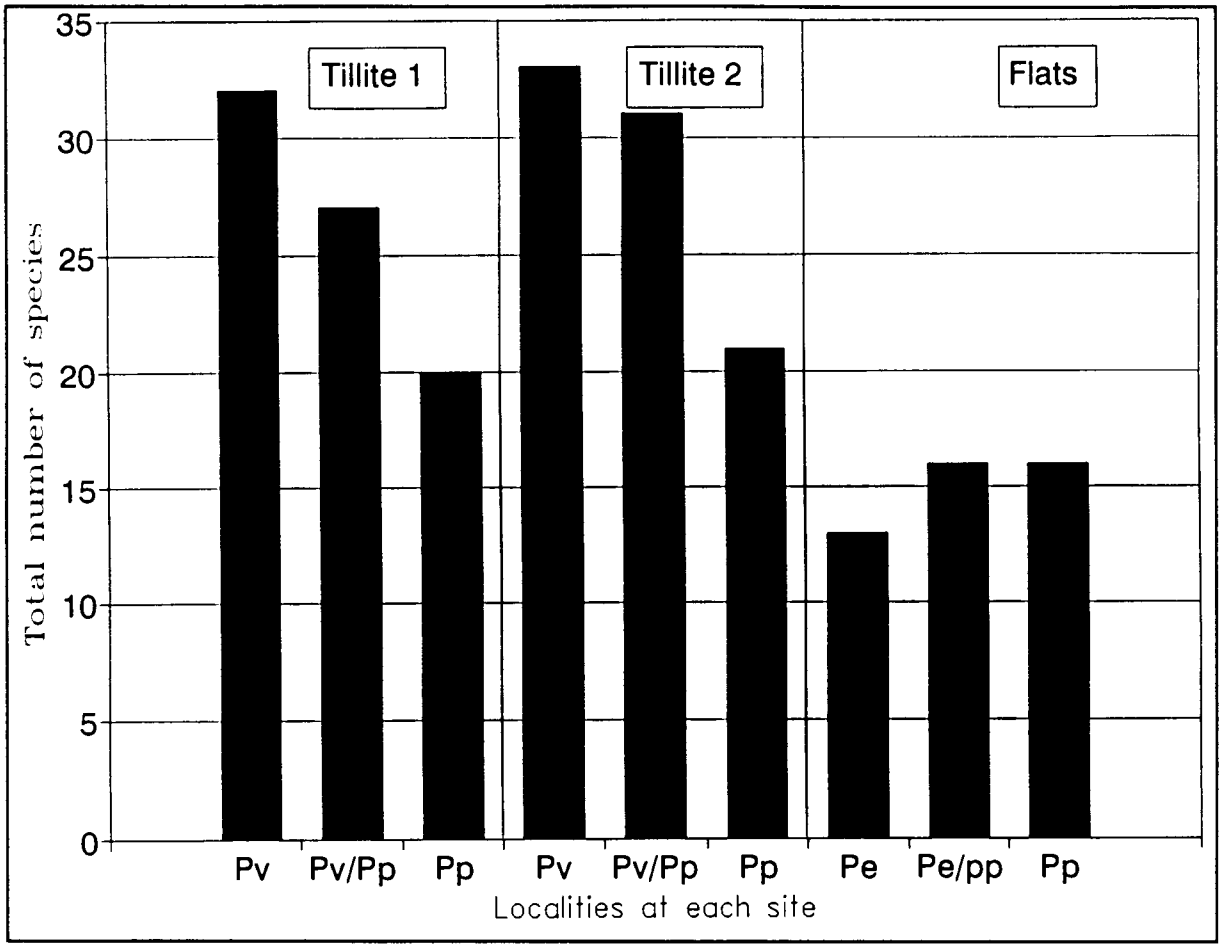

Figure 2-1. Total number of species recorded from three transects (tillite 1, tillite 2 and flats) along Pteronia replacement series at Tierberg in the Karoo. Data are totals from three 5 x 5 m^2 quadrats sampled at three localities at each site. Pv = P. viscosa present; Pv/Pp = boundary between Pv and Pp; Pp = P. pallens present; Pp/Pe = boundary between Pp and Pe; Pe = P. empetrifolia present.

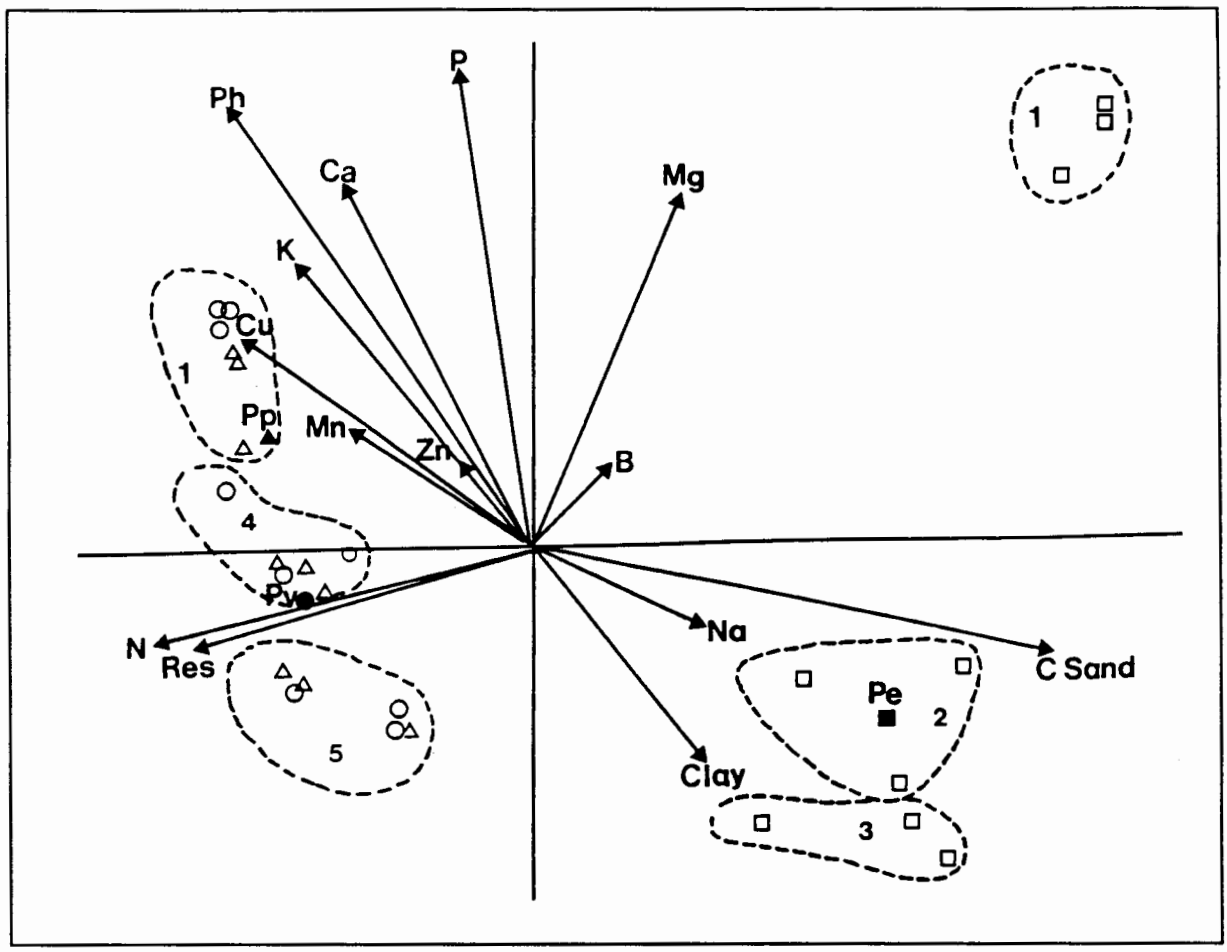

Figure 2-2. Species-soil biplot for axis 1 and 2 of a canonical correspondence analysis (CCA). Positions of quadrats for each site are shown as follows: (□) = flats; (△) = tillite 1; (○) = tillite 2. These represent the weighted average of all species present a particular quadrat. Positions of P. pallens (▲ Pp), P. cf. empetrifolia, (■ Pe) and P. viscosa (● Pv) are indicated according to their optimal abundances. Arrows indicate gradients of individual soil parameters are abreviated as follows: N = % total nitrogen; Res = resistance; Zn = zinc; Mn = manganese; Cu = copper; K = potassium; Ca = calcium; B = boron; Mg = magnesium; Na = sodium; cSand = % coarse sand and Clay = % clay. Long arrows represent important environmental variables which are more closely correlated with the ordination axes. Quadrats are grouped and numbered in the following manner: 1 = dominated by P. pallens; 2 = boundary between P. pallens and P. cf. empetrifolia on flats; 3 = dominated by P. empetrifolia; 4 = boundary between P. pallens and P. viscosa on tillite slopes and 5 = dominated by P. viscosa.

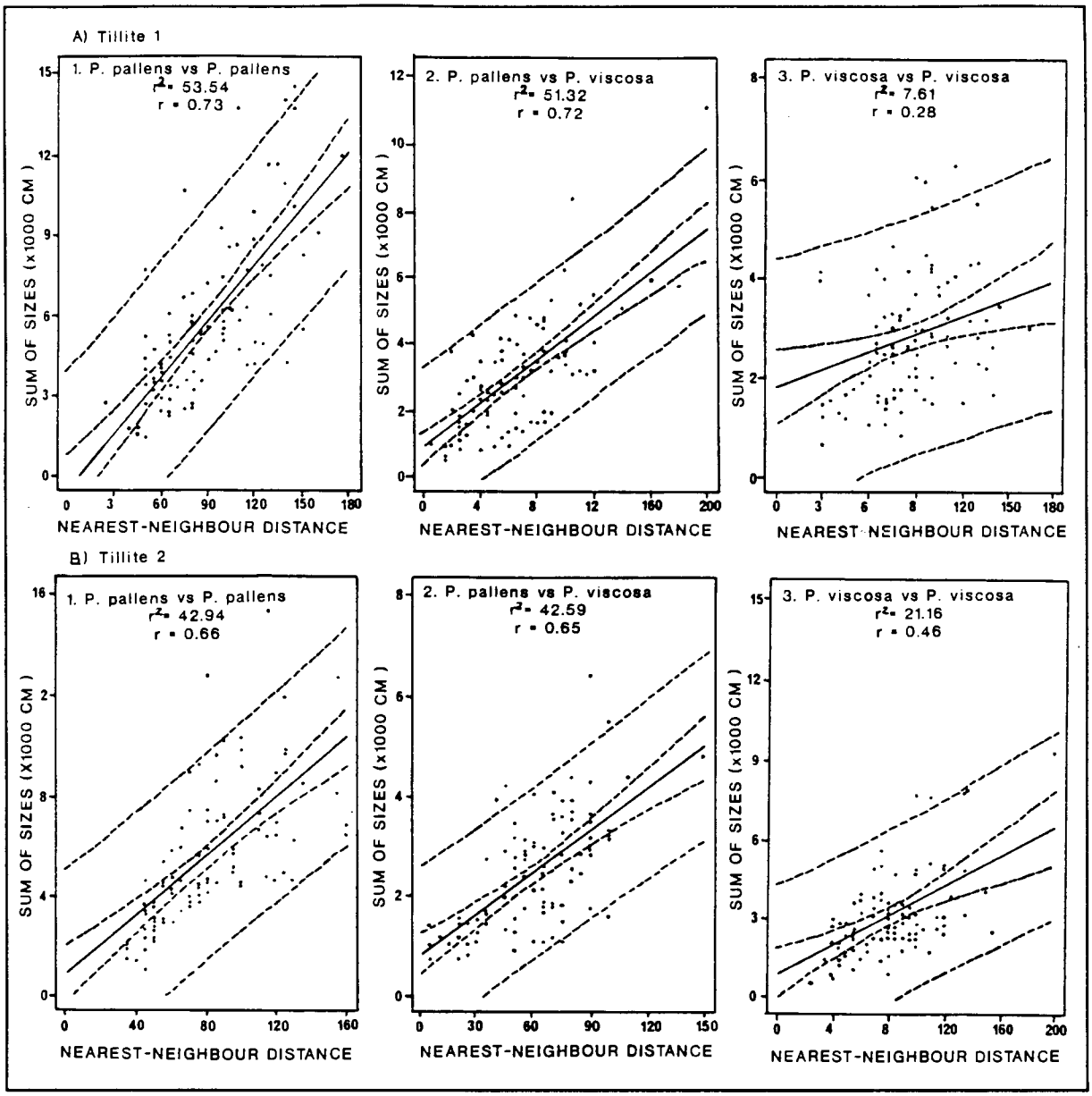

Figure 2-2a, 2-2b. Regression lines of nearest-neighbour distances against the sum of their sizes for 1) P. pallens - P. pallens, 2) P. pallens - P. viscosa and 3) P. viscosa - P. viscosa nearest-neighbour pairs from two sites a) tillite 1 and b) tillite 2 at the farm Tierberg in the Karoo.

2.5 DISCUSSION

From the nearest-neighbour analyses, some inferences can be made about the importance of competition in structuring karoo plant communities. A significant relationship between nearest-neighbour distances and the sum of nearest-neighbour plant covers indicates that a competitive inter-action may be occurring, and infers that the distance at which the species pairs establish, limits the size to which they grow. Results indicated that competitive interactions occur both at Pteronia-Pteronia population boundaries and within Pteronia populations. Correlation coefficients indicated that the strongest competitive relationships on the tillite slopes were between P. pallens-P. pallens and P. pallens-P. viscosa pairs and that the weakest relationships were between P. viscosa-P. viscosa pairs. The data thus indicated the existence of strong competitive interactions at population boundaries. Unfortunately, nearest-neighbour analysis does not allow one to draw conclusions as to the relative importance of edaphic specialisation and competition in structuring karoo plant communities.

Trends in soil physico-chemical properties over the Pteronia replacement series were also found (Table 2-1). These reflected community composition differences to some extent and indicated the existence of subtle edaphic gradients in addition to those reported by Midgely and Musil (1990) who studied the vegetation-soil relationships associated with *heuweltjies* and their surrounding vegetation.

The generally high correlation coefficients and high eigenvalues for the CCA indicated that the environmental variables accounted for much of the variation in species data (Table 2-2) - it must be noted that all species were considered in the ordinations; i.e. not only the Pteronia spp. The first axis of the CCA separated out the flats site from the tillite sites along a soil texture and chemical gradient. The first axis of both the CCA and DCA had similar eigenvalues, indicating that these environmental variables accounted for much of the variation in the species data along this axis. The eigenvalue for the second axis of the DCA was substantially lower than that obtained from the CCA, despite a high species-environment

correlation coefficient for the second CCA axis. This indicated that not all of the variation in the species data along this axis was explained by the measured edaphic variables. The second CCA axis separated out the different Pteronia spp. associations along a pH and nutrient gradient. Even though subtle edaphic gradients along these Pteronia replacement series did appear to exist, they were not sufficient to explain the replacement series. Soil pH was the only parameter that differed significantly across all three gradients. Soil pH is known to effect the rate of decomposition of soil organic material and availability of nutrients for plant uptake (Brady 1974). In this study, soil N and P levels along the Pteronia replacement series increased with increasing soil pH (Table 2-1). This increase in soil N and P fertility could partly explain the variation in Pteronia distributions.

Differences in site productivity could be inferred from the slopes of the nearest-neighbour regressions (R.I. Yeaton, pers. comm., Department of Botany, University of Natal, Pietermaritzburg). Regression slopes for P. pallens-P. pallens nearest-neighbour pairs lay above the slopes of P. viscosa-P. viscosa pairs. This indicates that, for plants of a given size, two P. pallens individuals occurred on average closer than two P. viscosa individuals. The fact that P. pallens occurs on more fertile sites with possibly higher soil moisture would explain why individuals of this species are able to grow closer together (Fig. 2-3) and are generally larger (Table 2-5). Regression slopes for the inter-specific pairs lay below the intra-specific nearest neighbour regression lines at both tillite sites. This indicates that inter-specific pairs of a given size grew closer together than intra-specific pairs.

Soil surface properties which affect soil water availability can also determine the spatial pattern of vegetation (Olsvig-Whittaker et al. 1983, Kadmon et al. 1989). In this study, P. pallens was more abundant in lower lying areas associated with drainage lines and around heuweltjies (Milton et al. 1992). It is possible that water availability may also determine Pteronia spp. distributions.

2.6 CONCLUSION

Although strong vegetation-soil relationships and inter- and intra-specific competitive interactions exist along Pteronia replacement series, the importance of biotic interactions in determining species distributions requires further investigation through laboratory competition studies and field transplant studies (it is, for example, possible that reproductive biology of the plants could explain the vegetation patterns). The question still remains: do biotic interactions drive vegetation dynamics as suggested in Yeaton and Esler (1990), or does the abiotic environment have a greater influence? The answer to species distribution patterns in the Karoo probably lies in an interaction between soil factors and competition.

2.7 REFERENCES

Acocks,J.P.H. 1975. Veld types of South Africa. Memoirs of Botanical Surveys of South Africa, No. 40. Government printer, Pretoria. 128pp.

Brady,N.C. 1974. The nature and properties of soils, MacMillan publishing Co.Inc., New York. 639pp.

Cody,M.L. 1986a. Spacing patterns in Mojave desert plant communities: near-neighbour analyses. Journal of Arid Environments 11:199-217.

Cody,M.L. 1986b. Spacing in Mojave desert plant communities. II. Plant size and distance relationships. Israel Journal of Botany 35:109-120.

Cowling,R.M., Gibbs Russell,G.E., Hoffman,M.T. and Hilton-Taylor,C. 1989. Patterns of plant species diversity in southern Africa. In: Biotic diversity in southern Africa: concepts and conservation, ed. B.J. Huntley, Oxford University Press, Cape Town. pp 19-50.

Dean,W.R.J. 1992. Effects of animal activity on the absorption rate of soils in the southern Karoo, South Africa. Journal of the Grassland Society of South Africa 9:178-180.

Fonteyn,P.J. and Mahall,B.E. 1981. An experimental analysis of structure in a desert plant community. Journal of Ecology 69:883-896.

Jürgens,N. 1986. Contributions to the ecology of southern African succulent plants. Mitteilungen aus dem Institut für Allgemeine Botanik 29:139-365.

Hill,M.O. and Gauch,H.G. 1980. Detrended correspondence analysis, an improved ordination technique. Vegetatio 42:47-58.

Kadmon,R., Yair,A. and Danin,A. 1989. Relationship between soil properties, soil moisture and vegetation along loess-covered hillslopes, Northern Negev, Israel. Catena supplement 14:43-57.

Key,L.J., Delph,L.J., Thompson,D.B. and Van Hoogenstyn,E.P. 1984. Edaphic factors and the perennial plant community of Sonoran desert bajada. Southwestern Naturalist 29:211-222.

Lloyd,J.W. 1989a. Discriminant analysis and ordination of vegetation and soils on the Vaalputs radioactive waste disposal site, Bushmanland, South Africa. South African Journal of Botany 55:127-136.

Lloyd,J.W. 1989b. Phytosociology of the Vaalputs radioactive waste disposal site, Bushmanland, South Africa. South African Journal of Botany 55:372-382.

Lovegrove,B.G. and Siegfried,W.R. 1986. Distribution and formation of mima-like earth mounds in the western Cape Province of South Africa. South African Journal of Science 82:432-436.

Midgely,G.F. and Musil,C.F. 1990. Substrate effects of zoogenic soil mounds on vegetation composition in the Worcester-Robertson valley, Cape Province. South African Journal of Botany 56:158-166.

Milton,S.J., Dean,W.R.J. and Kerley,G.I.H. 1992. Tierberg Karoo Research Centre: history, physical environment, flora and fauna. Transactions of the Royal Society of South Africa 48:15-46.

Olsvig-Whittaker,L. 1988. Relating small scale vegetation patterns to the environment. In: Diversity and pattern in plant communities, eds. H.J. During, M.J.A. Werger, and J.H. Willems, SPB Academic Publishing, The Hague. pp 87-94.

Olsvig-Whittaker,L., Shachak,M. and Yair,A. 1983. Vegetation patterns related to environmental factors in a Negev desert watershed. Vegetatio 54:153-165.

Palmer,A.R. 1991a. A syntaxonomic and synecological account of the vegetation of the eastern Cape Midlands. South African Journal of Botany 57:76-94.

Palmer,A.R. 1991b. Vegetation/environment relationships in the central area of the Cape Midlands, South Africa. Coenoses 6:29-38.

Palmer,A.R., Crook,B.J.S. and Lubke,R.A. 1988. Aspects of the vegetation and soil relationships in the Andries Vosloo Kudu Reserve, Cape Province. South African Journal of Botany 54:309-314.

Pielou,E.C. 1960. A single mechanism to account for regular, random and aggregated populations. Journal of Ecology 48:575-584.

Pielou,E.C. 1962. The use of plant-to-neighbour distances for the detection of competition. Journal of Ecology 50:357-367.

Rostagno,C.M., Del Valle,H.F. and Videla,L. 1991. The influence of shrubs on some chemical and physical properties of an aridic soil in north-eastern Patagonia, Argentina. Journal of Arid Environments 20:179-188.

Rutherford,M.C. and Westfall,R.H. 1986. Biomes of southern Africa - an objective categorisation. Memoirs of the Botanical Surveys of South Africa, no. 54. Government Printer, Pretoria. 98pp.

Smitheman,J. and Perry,P. 1990. A vegetation survey of the Karoo National Botanic Garden Reserve, Worcester. South African Journal of Botany 56:525-541.

Snijman,D. and Perry,P. 1987. A floristic analysis of the Nieuwoudtville Wild Flower Reserve, north-western Cape. South African Journal of Botany 53:445-454.

Stein,R.A. and Ludwig,J.A. 1979. Vegetation and soil patterns on a Chihuahuan desert bajada. American Midland Naturalist 101:28-37.

Ter Braak,C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167-1179.

Ter Braak,C.J.F. 1987a. CANOCO - a FORTRAN program for canonical community ordination by partial detrended canonical correspondence analysis, principal components analysis and redundancy analysis (version 2.1). Wageningen: TNO Institute of Applied Computer Science. 95pp.

Ter Braak,C.J.F. 1987b. The analysis of vegetation-environment relations by using canonical correspondence analysis. Vegetatio 69:69-77.

Ter Braak,C.J.F. 1987c. Ordination. In: Data analysis in community and landscape ecology, eds. R.G.H. Jongman, C.J.F. Ter Braak and O.F.R. Van Tongern. Pudoc, Wageningen. pp 91-193.

Visser,J.N.J. 1986. Geology. In: The Karoo biome: a preliminary synthesis, Part 1 - physical environment, eds. R.M. Cowling and P.W. Roux. South African National Scientific Programmes Report No. 124, Council for Scientific and Industrial Research, Pretoria. pp 70-95.

Wierenga,P.J., Hendrickx,J.M.H., Nash,M.H., Ludwig,J. and Daugherty,L.A. 1987. Variation of soil and vegetation with distance along a transect in the Chihuahuan desert. Journal of Arid Environments 13:53-63.

Yeaton,R.I. and Esler,K.J. 1990. The dynamics of a succulent karoo vegetation: a study of species association and recruitment. Vegetatio 88:103-113.

Zar,J.H. 1984. Biostatistical Analysis. Prentice-Hall, New Jersey, 2nd Edition. 718pp.

APPENDIX 2-8. Cover (m^2/m^2) of dominant species from three transects (tillite 1, tillite 2 and flats) along Pteronia replacement series at Tierberg in the Karoo. Data are means ± standard deviations from three 5 x 5 m^2 quadrats sampled at three localities at each site. Pv = P. viscosa present; Pv/Pp = boundary between Pv and Pp; Pp = P. pallens present; Pp/Pe = Boundary between Pp and Pe; Pe = P. empetrifolia present. Ranked abundance is shown in brackets where 1 = species with the highest number of individuals.

Site	total spp	Dominant species	Cover	Ranked abundance
Tillite 1				
Pv	32	Chrysocoma ciliata	0.068 ± 0.013	(1)
		Ruschia spinosa	0.043 ± 0.003	(3)
		Eriocephalus ericoides	0.028 ± 0.000	(4)
		Pteronia viscosa	0.028 ± 0.003	(7)
		Rhigozum obovatum	0.022 ± 0.024	(16)
Pv/Pp	27	Pteronia pallens	0.070 ± 0.008	(3)
		Rhigozum obovatum	0.046 ± 0.005	(10)
		Ruschia spinosa	0.027 ± 0.001	(7)
		Pteronia viscosa	0.022 ± 0.017	(8)
		Chrysocoma ciliata	0.015 ± 0.006	(2)
Pp	20	Pteronia pallens	0.132 ± 0.022	(2)
		Rhigozum obovatum	0.020 ± 0.026	(7)
		Ruschia crassa	0.009 ± 0.009	(5)
		Chrysocoma ciliata	0.006 ± 0.005	(4)
		Pentzia incana	0.003 ± 0.004	(10)
Tillite 2				
Pv	33	Ruschia spinosa	0.072 ± 0.050	(3)
		Rhigozum obovatum	0.069 ± 0.012	(5)
		Pteronia viscosa	0.029 ± 0.005	(4)
		Pentzia incana	0.027 ± 0.005	(2)
		Lycium shizocaylx	0.016 ± 0.007	(17)

Site	total spp	Dominant species	Cover	Ranked abundance
Pv/Pp	31	Pteronia pallens	0.050 ± 0.017	(2)
		Pteronia viscosa	0.029 ± 0.009	(4)
		Pentzia incana	0.018 ± 0.016	(3)
		Lycium shizocaylx	0.015 ± 0.021	(23)
		Rhigozum obovatum	0.014 ± 0.020	(12)
Pp	21	Pteronia pallens	0.198 ± 0.041	(1)
		Sphalmanthus bijliae	0.012 ± 0.003	(2)
		Zygophyllum sp	0.008 ± 0.001	(5)
		Lycium shizocaylx	0.006 ± 0.004	(12)
		Aridaria noctiflora	0.006 ± 0.006	(6)
Flats				
Pe	13	Galenia fruticosa	0.073 ± 0.030	(1)
		Ruschia spinosa	0.073 ± 0.075	(2)
		Osteospermum sinuatum	0.031 ± 0.002	(5)
		Pteronia empetrifolia	0.021 ± 0.010	(6)
		Herreroa latipetala	0.018 ± 0.015	(4)
Pe/Pp	16	Ruschia spinosa	0.067 ± 0.040	(3)
		Herreroa latipetala	0.050 ± 0.015	(1)
		Pteronia pallens	0.038 ± 0.015	(7)
		Galenia fruticosa	0.029 ± 0.020	(2)
		Drosanthemum montaguense	0.027 ± 0.030	(5)
		Pteronia empetrifolia	0.020 ± 0.002	(8)
Pp	16	Pteronia pallens	0.096 ± 0.003	(2)
		Ruschia spinosa	0.091 ± 0.028	(1)
		Galenia fruticosa	0.019 ± 0.015	(4)
		Herreroa latipetala	0.011 ± 0.005	(3)
		Brownanthus ciliatus	0.007 ± 0.009	(7)

CHAPTER 3

THE COMPARISON OF SELECTED LIFE-HISTORY CHARACTERISTICS OF MESEMBRYANTHEMA SPECIES OCCURRING ON AND OFF MIMA-LIKE MOUNDS (*HEUWELTJIES*)

3.1 ABSTRACT

Selected life-history characteristics of Mesembryanthema species occurring on and off mima-like mounds (*heuweltjies*) were compared at Tierberg in the southern Succulent Karoo, South Africa. Seed production, the number of seeds retained in seed capsules and germination behaviour were measured in fourteen species of Mesembryanthema which were representatives of two sub-families: the Ruschioideae and the Mesembryanthemoideae. Species occurring on *heuweltjies* had low overall germination and high seed retention compared with those species occurring off *heuweltjies*. A strong negative correlation was found between the degree of seed retention and maximum germination. It was proposed that rapid germination and low seed dormancy in species occurring on the flats would be a viable strategy where competition for safe recruitment sites is strong. Species occurring on the flats are long-lived woody shrubs, thus the resulting high levels of seedling mortality probably do not have a major impact on population dynamics. *Heuweltjies* are sites of intense disturbance. Plant species that occur on *heuweltjies* can also occur off *heuweltjies* in disturbed vegetation. Opportunistic life-history characteristics allow these species to colonise disturbed areas. *Heuweltjie* species thus act as pioneers in a successional process which results ultimately in the re-colonisation of the long-lived flats species. Phylogenetic factors may also determine the species distributions. Members of the Mesembryanthemoideae did not occur off *heuweltjies* in undisturbed areas. Most Ruschioideae were found on the flats but the few species that occurred on *heuweltjies* shared similar characteristics with the Mesembryanthemoideae. The primitive life-history characteristics exhibited by the Mesembryanthemoideae enable them to exploit disturbed conditions.

3.2 INTRODUCTION

The Succulent Karoo of southern Africa has an interesting source of heterogeneity associated with *heuweltjies* (phonetic pronunciation: hear-vill-keys) which resemble the mima-like mounds of North America (Cox 1984). The distribution of these circular soil mounds largely coincides with the distribution of the Succulent Karoo (Lovegrove and Siegfried 1986). *Heuweltjies* have a different soil chemistry and support a different biota from their adjacent surroundings (e.g. Midgely and Musil 1990, Dean and Yeaton in press). In very disturbed areas, *heuweltjie* species are able to colonise the surrounding vegetation (Milton et al. 1992). Disturbance levels on *heuweltjies* are higher than in surrounding vegetation (i.e. the disturbances occur less often off-*heuweltjies*); they are foci for foraging by domestic stock (Armstrong and Siegfried 1990), burrowing by rodents (Milton et al. 1992) and are frequently used as dung middens by some mammal species (Milton and Dean 1990a). More importantly, they are sites of termite colonisation. Although it is now generally accepted that termites are responsible for the creation of *heuweltjies* (Milton and Dean 1990a), the origins of these mounds have been the centre of much debate in the past (e.g. Lovegrove and Siegfried 1986, Cox et al. 1987, Lovegrove and Siegfried 1989, Milton and dean 1990a, Moore and Picker 1991). *Heuweltjies* no doubt influence diversity at a landscape level (Milton and Dean 1990a). They also may play an important role in the dynamics of the vegetation associated with them. Yeaton and Esler (1990) suggested that *heuweltjies* provide a source of disturbance which initiates the successional processes within these communities. An understanding of the reproductive attributes of the dominant species occurring on and off *heuweltjies* may assist in the understanding of the successional processes in this landscape.

The Succulent Karoo has an exceptionally rich flora (Cowling et al. 1989) which includes 36% of the world's succulents (Cowling et al. submit.). Of particular interest is the Mesembryanthema group (Family Aizoaceae, Hartmann 1991) which is represented by over 2 000 species and is principally confined to the winter

rainfall semi-arid and arid regions of southern Africa (Cowling et al. 1989, Cowling et al. submit.). The wide range of habitats occupied by the Mesembryanthema in these areas (Jürgens 1986) and the fact that several species often coexist in the same community (Cowling et al. submit.) means that comparative life-history studies can be done with relative ease (Krebbs and Davies 1981).

The life-history characteristics which are of particular interest in the Mesembryanthema are those related to seed germination and dispersal. The Mesembryanthema are interesting in that most species have characteristic hygrochastic capsules (Hartmann 1988) which open during rain to release seeds when moisture conditions are favourable for germination and seedling establishment (Garside and Lockyer 1930, Lockyer 1932, Ihlenfeldt 1971, Van Rooyen et al. 1980, Gutterman 1990, Hartmann 1991). Different capsule designs have evolved within this family "to promote the extension of dispersal in time" (Hartmann 1991). The absence of dispersal-enhancing characteristics and/or adaptations which hinder dispersal, are common in plants growing in arid environments (Ellner and Shmida 1981). The ability to ensure that only part of the seed population germinates at any one time, either by controlling seed release or germination behaviour, may be the key to the success of the Mesembryanthema in the Karoo (Van Rooyen et al. 1990). In this semi-arid region, rainfall events are spatially and temporally variable, prolonged droughts are common (Booysen and Rowswell 1983, Werger 1986) and competition is strong (Yeaton and Esler 1990).

In this chapter, selected life-history characteristics of Mesembryanthema species occurring on and off *heuweltjies* were compared. The following hypothesis was investigated:

> **Species commonly occurring on *heuweltjies* and in other disturbed environments should display opportunistic life history characteristics** (see Gadgil and Solbrig 1972).

Heuweltjie species tend to invade degraded vegetation. Maintaining high degrees of seed dormancy or confining germination to a relatively narrow range of conditions, and retaining seeds for long periods in capsules, are some strategies that could be employed by Mesembryanthema to spread or confine the risk of recruitment failure in disturbed environments. Species occurring on *heuweltjies* tend to be short lived. There is also a high probability that seedlings of these species will die from disturbance. Cohen (1966, 1967) used probability models to predict certain evolutionary responses (in annuals) to increasing environmental uncertainty. He concluded that the optimal number of seeds committed to germination would decrease as the probability of a successful outcome decreased. Thus, increased environmental uncertainty on *heuweltjies* associated with disturbance may have resulted in adaptations in Mesembryanthema which spread the risk of germination in time (either by seed retention or seed dormancy). The turnover of plant communities off *heuweltjies* is considerably slower and adult plant populations tend to be long-lived and stable (B. Bayer, pers. comm., Worcester Veld Reserve, Worcester; Yeaton and Esler 1990). Recruitment sites in this environment are limited because adult plants tend to occupy them. It is less easy to predict what this would mean for germination and dispersal characteristics. Species off *heuweltjies* may have more competitive life history strategies (since the "winner" would take all). One strategy to increase the probability of recruitment success is to increase the rate of seed release. The aims of this chapter were:

1. to compare seed production, retention and germination of species occurring on and off *heuweltjies* and
2. to concentrate on the life-history characteristics of the Mesembryanthema, since the ecology of this group is poorly understood.

Clearly, phylogeny is an important consideration in life-history studies, but by confining the research to a variety of co-occurring species within a single family, an attempt was made to avoid some of these confounding factors. If closely related species behave differently, one can assume that these differences have

evolved in relation to different ecological pressures. Phylogenetic characteristics were, however, still accounted for at the sub-family level in this chapter.

3.3 STUDY SITE AND STUDY SPECIES

The study was conducted at the Tierberg Karoo Research Centre (Milton et al. 1992) near Prince Albert in the Succulent Karoo (33°10'S, 22°17'E). The area is situated on a colluvial plain (800m altitude), 20 km north of the Swartberg Mountains in the Cape Folded Belt. The area receives approximately 170 mm of rain per year, with marked autumn and minor spring peaks. Seventy percent of the vegetation on the 100 ha site is relatively homogeneous, comprising perennial succulent (mostly Mesembryanthema) and non-succulent shrubs (Milton et al. 1992). This vegetation is referred to as the "flats". The rest of the area is occupied by *heuweltjies* (Lovegrove and Siegfried 1986) and drainage lines. *Heuweltjies* support a set of species distinct from the surrounding vegetation (Armstrong and Siegfried 1990). These nutrient-rich patches, with high concentrations of organic matter, nutrients and salts (Milton et al. 1992), average about 13 m in diameter and are fairly evenly distributed over the study site at a mean density of 2.33 ± 0.11 *heuweltjies* ha^{-1} (Milton et al. 1992). There is often no distinct elevational difference between *heuweltjies* and "flats", although occasionally the former are slightly raised (10 cm) as mounds. The study site has been protected from domestic herbivory since 1987. Prior to this date, the area was moderately grazed by sheep (Milton et al. 1992).

Twenty-five species of Mesembryanthema occur on the study site. All of these species are dwarf or low evergreen leaf succulents with similar growth forms and belong to two sub-families which comprise the Mesembryanthema (Ruschioideae and Mesembryanthemoideae in the family Aizoaceae, Bittrich and Hartmann 1988, Hartmann 1991). Twelve of the more common species were studied (Table 3-1). Of the five species sampled on the flats, none belonged to the sub-family

Mesembryanthemoideae. In contrast, members of the sub-family Ruschioideae occupy a range of habitats on the study site. Two of the Ruschioideae species that were sampled were found on *heuweltjies* and five were found on the flats of the study site (Table 3-1). Both the tall and the short growth forms of Ruschia spinosa (Chapter 1) were sampled.

Table 3-1. List of study species, sampled in two habitats; F = flats (i.e. off *heuweltjie* vegetation), H = *heuweltjies*.

	Habitat
Mesembryanthemoideae	
Aridaria noctiflora (L.) Schwant.	H
Brownanthus ciliatus (Ait.) Schwant.	H
Mesembryanthemum cf. crystallinum L.	H
Psilocaulon utile L.Bol.	H
Sphalmanthus brevifolius (Haw.) N.E.Br.	H
Ruschiodeae	
Drosanthemum cf. hispidum (L.) Schwant.	H
Drosanthemum montaguense L.Bol.	F
Hereroa latipetala L.Bol.	F
Malephora lutea Schwant.	H
Rhinephyllum cf. graniforme (Haw.) L.Bol.	F
Rhinephyllum macradenium (L. Bol.) Schwant.	F
Ruschia spinosa (L.) H.E.K. Hartm. & Stuber.	F

3.4 METHODS

3.4.1 Seed production and seed retention

Data for the number of capsules per plant were obtained from Milton and Dean (1990b). Missing data were supplemented by capsule counts in February 1990 (from n = 10 plants of each species). Due to lack of individuals for sampling, capsule numbers for Mesembryanthemum crystallinum had to be estimated using counts from two plants.

In order to quantify seed retention, seed capsules of each species were collected

over a period of seven months from December 1989 to June 1990. At each collection period, 20 seed capsules were harvested from ten, randomly selected plants of each species and the number of seeds per capsule was determined. Flowering of most Mesembryanthema species occurs during spring (September to November) although some species show an opportunistic response to rain events (Hoffman 1989, Milton 1992). It was noted during sampling that some of the *heuweltjie* species had extended flowering periods (e.g. Aridaria noctiflora and Sphalmanthus brevifolius). By December/January most species had "ripe" capsules (i.e. seeds were ready for dispersal). An attempt was made to collect the first batch of capsules prior to major rain events, although by 31 January 1990 (the first collection date for many species), 32 mm of rain had already fallen. Rainfall data were obtained from an automatic weather station established on the study site (W.R.J. Dean, pers. comm., Fitzpatrick Institute, University of Cape Town). Fresh seeds from the first sampling period were retained for germination trials. As an indication of capsule size, closed capsule diameters were measured from ten, randomly selected capsules taken from the first sampling period.

3.4.2 Germination

Twenty five seeds were sown in each of four petri dishes (diameter 9 mm) containing three layers of Schleicher & Schuell filter paper saturated with a 0.75 $g.l^{-1}$ solution of Benlate fungicide (to prevent fungal infection). Petri dishes were then placed in clear plastic bags in controlled environment cabinets with a photon flux density of 49 $\mu mol\ m^{-2}s^{-1}$. The two cabinets were set at an alternating temperature/light cycle designed to simulate average day and night temperatures in summer (30°C, 14 hr light period and 15°C, 10 hr dark period) and winter (20°C, 14 hr light period and a 10°C, 10 hr dark period). Seeds were considered germinated when the radicle had emerged and elongated to 2 mm. Numbers of germinated seeds were recorded at two day intervals for a month after initiation of the

germination trials. In previous germination experiments it was established that most non-dormant Mesembryanthema seeds germinated within a month (unpublished data).

3.4.3 Statistical analysis

Generalised linear modelling (statistical package: GLIM, Baker and Nelder 1978) was performed on the germination and seed retention data. This method avoids the assumptions of normality associated with parametric statistics (Zar 1984). A logit-linear model was fitted to the germination data using a binomial error distribution using a logit-link function. The effects of temperature, habitat and taxonomic status on germination were tested. A log-linear model was fitted to the seed retention data using a Poisson error distribution and a log link (McCullagh and Nelder 1983). In this case the effects of habitat and family on seed retention were tested. Where variation in the seed retention data were more than that described by the Poisson distribution, an over-dispersion parameter was introduced. In the case of extra-binomial variation, the Williams (1982) procedure was applied. Results are presented in an analysis of deviance table. The GLIM term, deviance means something analogous to a residual sum of squares in a regression analysis. The change in deviance indicates the degree to which a predictor variable can explain the data.

Simple linear regressions (on seed production data), Spearman rank correlations (on seed retention versus seed germination data), and Mann-Whitney tests (on seed production and germination data) were computed using Statgraphics 5.0 (STSC Inc.).

3.5 RESULTS

3.5.1 Seed production

The number of capsules per plant varied widely between species (Table 3-2), although the range was much greater on *heuweltjies*, with some species producing over 150 capsules per individual. The number of seeds per capsule also varied considerably between species (Table 3-2). Seeds of species occurring on the flats were all relatively small, and although there were no significant differences in seed size of species occurring off and on *heuweltjies* ($t = -1.55$, N.S.), there was greater variation in seed size in the species occurring on *heuweltjies*.

3.5.2 Germination

Overall germination percentages were exceptionally low for species occurring on *heuweltjies* (Table 3-3). For all trials involving *heuweltjie* species, germination success was less than 25% (Table 3-3). Although the trend was for higher overall germination percentages of *heuweltjie* species under the temperature regime which simulated summer conditions (except Drosanthemum hispidum and Brownanthus ciliatus), these differences were only significant for Aridaria noctiflora (Table 3-3). Significantly higher overall germination percentages were obtained for species occurring on the flats (Table 3-3). The trend for these species was for lower overall germination percentages under a temperature regime which simulated summer conditions and in some, but not all, cases these differences were significant (Table 3-3). Although differences in germination percentages could be accounted for by habitat, phylogeny also had to be considered. A generalised linear model (binomial distribution, logit-link) of the overall germination percentages of all of the species studied indicated that habitat accounted for much more variation in the data than did taxonomic status, although the latter still accounted for some variation (Table 3-4).

3.5.3 Seed Retention

Seed release from capsules was generally rapid in species occurring on the flats, and after three to four months (and 58 mm of rain), few seeds remained in the capsules (Table 3-5). Species on the *heuweltjies* had significantly higher percentages of seeds remaining in the capsules than flats species (Mann-Whitney test, $Z = 2.93$, $P < 0.003$)(Fig. 3-1). Although differences in seed retention could be accounted for by habitat, phylogeny (sub-family) also had to be considered. A generalised linear model (Table 3-6) on degree of seed retention (i.e. the percentage of seed remaining after 177.5 mm of rain) indicated that habitat explained most of the variation in the data. Phylogeny did not explain any of the variation in the data.

A Spearman rank correlation of the maximum percentage germination (Table 3-3) versus the degree of seed retention (as measured by the percentage of seeds remaining in capsules after six months and 177.5 mm of rain, Table 3-5) for each study species yielded a significant negative relationship ($P \leq 0.05$, d.f. = 12, coefficient = 0.688).

Table 3-2. Capsule numbers per plant[1], capsule sizes (n = 10 capsules), number of seeds per capsule (n = 20 capsules), number of seeds per plant and seed size (n = 10 seeds) for 13 species of Mesembryanthema at the Tierberg Karoo Research Centre. Data are means ± standard errors. - = missing data.

	CAPSULES/ PLANT[1]	CAPSULE DIAMETER (mm)	SEEDS/ CAPSULE	SEEDS/ PLANT	SEED SIZE[2] (mm^2)
FLATS SPECIES					
Drosanthemum montaguense	47.0 ± 2.0	4.8 ± 0.1	81.1 ± 6.2	3809	0.54
Hereroa latipetala	1.7 ± 0.2	8.9 ± 0.3	387.4 ± 69.3	659	0.42
Rhinephyllum cf. graniforme	14.2 ± 2.7*	4.5 ± 0.2	65.6 ± 11.2	931	0.26
Rhinephyllum macradenium	4.5 ± 0.3	8.4 ± 0.3	113.9 ± 11.8	513	-
Ruschia approximata	30.0 ± 8.0	4.9 ± 0.1	94.0 ± 6.4	2819	0.32
Ruschia spinosa (short)	17.4 ± 3.5	4.5 ± 0.1	27.4 ± 11.0	476	0.59
***HEUWELTJIE* SPECIES**					
Aridaria noctiflora	41.8 ± 8.9	6.6 ± 0.2	19.8 ± 3.8	826	1.58
Brownanthus ciliatus	187.0 ± 27.0	3.8 ± 0.1	26.9 ± 2.0	5021	0.57
Drosanthemum hispidum	49.0 ± 3.0*	4.3 ± 0.2	30.6 ± 5.0	1497	0.26
Malephora latipetala	5.7 ± 0.5	7.3 ± 0.1	86.5 ± 7.3	493	0.60
Mesembryanthemum crystallinum	~50*	13.6 ± 0.5	120.1 ± 20.5	6004	0.60
Psilocaulon utile	178.0 ± 3.0	3.4 ± 0.2	17.5 ± 2.5	3106	0.60
Sphalmanthus brevifolius	42.0 ± 8.0	7.2 ± 0.4	26.2 ± 4.0	1101	2.08

[1] Data from Milton and Dean (1990b), except for those indicated by a * (this study)

[2] Seed area was used as an approximation of seed size: long axis x short axis (mm^2).

Table 3-2. Capsule numbers per plant[1], capsule sizes (n = 10 capsules), number of seeds per capsule (n = 20 capsules), number of seeds per plant and seed size (n = 10 seeds) for 13 species of Mesembryanthema at the Tierberg Karoo Research Centre. Data are means ± standard errors. - = missing data.

	CAPSULES/ PLANT[1]	CAPSULE DIAMETER (mm)	SEEDS/ CAPSULE	SEEDS/ PLANT	SEED SIZE[2] (mm^2)
FLATS SPECIES					
Drosanthemum montaguense	47.0 ± 2.0	4.8 ± 0.1	81.1 ± 6.2	3809	0.54
Hereroa latipetala	1.7 ± 0.2	8.9 ± 0.3	387.4 ± 69.3	659	0.42
Rhinephyllum cf. graniforme	14.2 ± 2.7*	4.5 ± 0.2	65.6 ± 11.2	931	0.26
Rhinephyllum macradenium	4.5 ± 0.3	8.4 ± 0.3	113.9 ± 11.8	513	-
Ruschia approximata	30.0 ± 8.0	4.9 ± 0.1	94.0 ± 6.4	2819	0.32
Ruschia spinosa (short)	17.4 ± 3.5	4.5 ± 0.1	27.4 ± 11.0	476	0.59
***HEUWELTJIE* SPECIES**					
Aridaria noctiflora	41.8 ± 8.9	6.6 ± 0.2	19.8 ± 3.8	826	1.58
Brownanthus ciliatus	187.0 ± 27.0	3.8 ± 0.1	26.9 ± 2.0	5021	0.57
Drosanthemum hispidum	49.0 ± 3.0*	4.3 ± 0.2	30.6 ± 5.0	1497	0.26
Malephora latipetala	5.7 ± 0.5	7.3 ± 0.1	86.5 ± 7.3	493	0.60
Mesembryanthemum crystallinum	~50*	13.6 ± 0.5	120.1 ± 20.5	6004	0.60
Psilocaulon utile	178.0 ± 3.0	3.4 ± 0.2	17.5 ± 2.5	3106	0.60
Sphalmanthus brevifolius	42.0 ± 8.0	7.2 ± 0.4	26.2 ± 4.0	1101	2.08

[1] Data from Milton and Dean (1990b), except for those indicated by a * (this study)

[2] Seed area was used as an approximation of seed size: long axis x short axis (mm^2).

Table 3-3. Percentage germination (after 30 days) of freshly collected seed of thirteen species of Mesembryanthema occurring on and off *heuweltjies* at the Tierberg Karoo Research Centre, Cape Province, South Africa. Seeds were germinated at two temperature regimes: 10°C night / 20°C day and 15°C night / 30°C day, simulating spring/autumn and summer conditions respectively. Data are means ± standard errors from n = 4 petri-dishes each containing 25 seeds. Mann-Whitney tests for independent samples were used to test for temperature effects and for the differences between germination of species on and off *heuweltjies*. N.S. = non-significant, * = $P < 0.05$, ** = $P < 0.01$.

	PERCENTAGE GERMINATION				
	10/20	15/30	Z	Prob	Sig.
FLATS SPECIES					
Drosanthemum montaguense	97.0 ± 1.9	21.0 ± 3.0	2.23	0.03	*
Hereroa latipetala	100.0 ± 0.0	100.0 ± 0.0	-	-	
Rhinephyllum cf. graniforme	65.0 ± 6.2	78.0 ± 8.1	0.74	0.46	N.S
Rhinephyllum macradenium	86.0 ± 2.3	76.0 ± 6.3	0.88	0.38	N.S
Ruschia approximata	80.0 ± 1.7	98.0 ± 1.2	2.20	0.03	*
Ruschia spinosa (short)	82.0 ± 2.6	54.0 ± 8.9	2.03	0.04	*
Ruschia spinosa (tall)	88.0 ± 2.9	55.0 ± 1.9	2.19	0.03	*
***HEUWELTJIE* SPECIES**					
Aridaria noctiflora	22.0 ± 4.8	42.0 ± 7.4	2.19	0.03	*
Brownanthus ciliatus	5.0 ± 1.0	0.0 ± 0.0	-	-	
Drosanthemum hispidum	3.0 ± 1.0	0.0 ± 0.0	-	-	
Malephora latipetala	3.0 ± 1.9	6.0 ± 4.8	0	1	N.S.
Mesembryanthemum cf. crystallinum	0.0 ± 0.0	0.0 ± 0.0	-	-	
Psilocaulon utile	5.0 ± 2.5	7.0 ± 3.4	0.30	0.77	N.S.
Sphalmanthus brevifolius	11.0 ± 3.0	17.0 ± 6.2	0.74	0.46	N.S.
Z-statistic	3.07	2.95			
Probability of exceeding Z	0.002	0.003			
Significance	**	**			

Table 3-4. Analysis of deviance table obtained by generalised linear interactive modelling on percent germination data (Table 3-2) of 13 species of Mesembryanthema from the Tierberg Karoo Research Centre, Cape Province, South Africa. Relationships between temperature, habitat (*heuweltjie* vs off *heuweltjie*), family (Mesembryanthemoideae vs Ruschioideae) and species (13 species) and germination were sought.

MODEL	RESIDUAL DEVIANCE	D.F.	X^2	DEVIANCE CHANGE	D.F.
mean	8724.6	111			
mean + temperature	8673.9	110	6886	50.8	1
mean + habitat	2737.7	110	2782	5987	1
mean + family	5830.2	110	4916	2894	1
mean + species	1371.8	98	1210	7353	13
all main effects	1262.1	97	1159	7463	14

Table 3-5. The number of seeds retained in Mesembryanthema capsules collected from the Tierberg Karoo Research Centre. Data are numbers of seeds per capsule (n = 20) ± standard deviations. Capsules were collected from the same area over a six month period. % Rem = percentage of seed remaining after six months and 177.5 mm of rain (initial numbers were taken from the December 12 or January 31 data). - = missing data.

	DEC 12	JAN 31	MAR 7	MAR 24	APR 4	APR 22	JUN 11
RAIN PRIOR TO COLLECTION (mm)	**0**	**32**	**58**	**13**	**0**	**46**	**28.5**
FLATS SPECIES							
Drosanthemum montaguense	unripe	81.1 ± 27.7	7.4 ± 4.9	1.9 ± 2.7	4.7 ± 3.0	3.9 ± 2.8	3.2 ± 3.6
Hereroa latipetala	unripe	387.4 ± 229.9	9.7 ± 17.3	21.7 ± 41.3	28.6 ± 64.7	1.0 ± 2.0	2.9 ± 6.3
Rhinephyllum cf. graniforme	unripe	65.6 ± 50.0	2.0 ± 4.0	9.0 ± 0.2	0.2 ± 0.4	0.0 ± 0.0	0.0 ± 0.0
Rhinephyllum macradenium	113.9 ± 64.4	-	0.5 ± 1.0	0.4 ± 1.0	1.0 ± 2.0	0.0 ± 0.0	0.0 ± 0.0
Ruschia approximata	93.9 ± 28.4	-	20.6 ± 6.9	15.3 ± 8.7	15.0 ± 9.1	6.3 ± 7.6	7.3 ± 5.9
Ruschia spinosa (short)	-	-	2.6 ± 2.3	1.4 ± 1.7	1.7 ± 1.6	1.1 ± 1.5	0.7 ± 1.0
Ruschia spinosa (tall)	27.4 ± 11.0	-	3.2 ± 3.1	1.2 ± 1.8	0.9 ± 1.5	0.2 ± 0.4	0.4 ± 0.6
***HEUWELTJIE* SPECIES**							
Aridaria noctiflora	unripe	19.8 ± 17.1	22.4 ± 24.4	3.0 ± 3.0	6.0 ± 4.5	5.4 ± 3.0	3.3 ± 2.0
Brownanthus ciliatus	unripe	26.9 ± 8.8	2.1 ± 1.6	1.8 ± 1.3	2.8 ± 1.5	4.5 ± 3.2	2.2 ± 1.6
Drosanthemum hispidum	30.6 ± 22.0	-	-	-	-	-	15.5 ± 6.2
Malephora latipetala	unripe	86.5 ± 32.8	24.3 ± 18.1	41.3 ± 21.1	25.0 ± 16.2	20.4 ± 2.0	6.3 ± 26.3
Psilocaulon utile	unripe	unripe	17.5 ± 11.2	6.3 ± 2.9	6.2 ± 2.9	4.2 ± 1.8	2.7 ± 3.3
Sphalmanthus brevifolius	unripe	26.2 ± 17.8	26.2 ± 17.8	5.9 ± 7.7	9.6 ± 7.9	5.2 ± 4.3	4.2 ± 2.7

Table 3-6. Analysis of deviance table obtained by generalised linear interactive modelling on seed retention data (percentage of seed remaining after six months and 177.5 mm of rain, Table 3-4) of 13 species of Mesembryanthema from the Tierberg Karoo Research Centre, Cape Province, South Africa. Relationships between habitat (*heuweltjie* vs off *heuweltjie*) and family (Mesembryanthemoideae vs Ruschioideae) were sought.

MODEL	RESIDUAL DEVIANCE	D.F.	X^2	DEVIANCE CHANGE
mean	196.07	12		
mean + habitat[1]	66.85	11	71.82	129.3
mean + family	193.67	11	237.4	2.4

[1] Final model:

$$Log\ \mu = \mu + \alpha^{habitat}$$

Scale factor = 6.53
Final deviance = 10.23, d.f. = 11

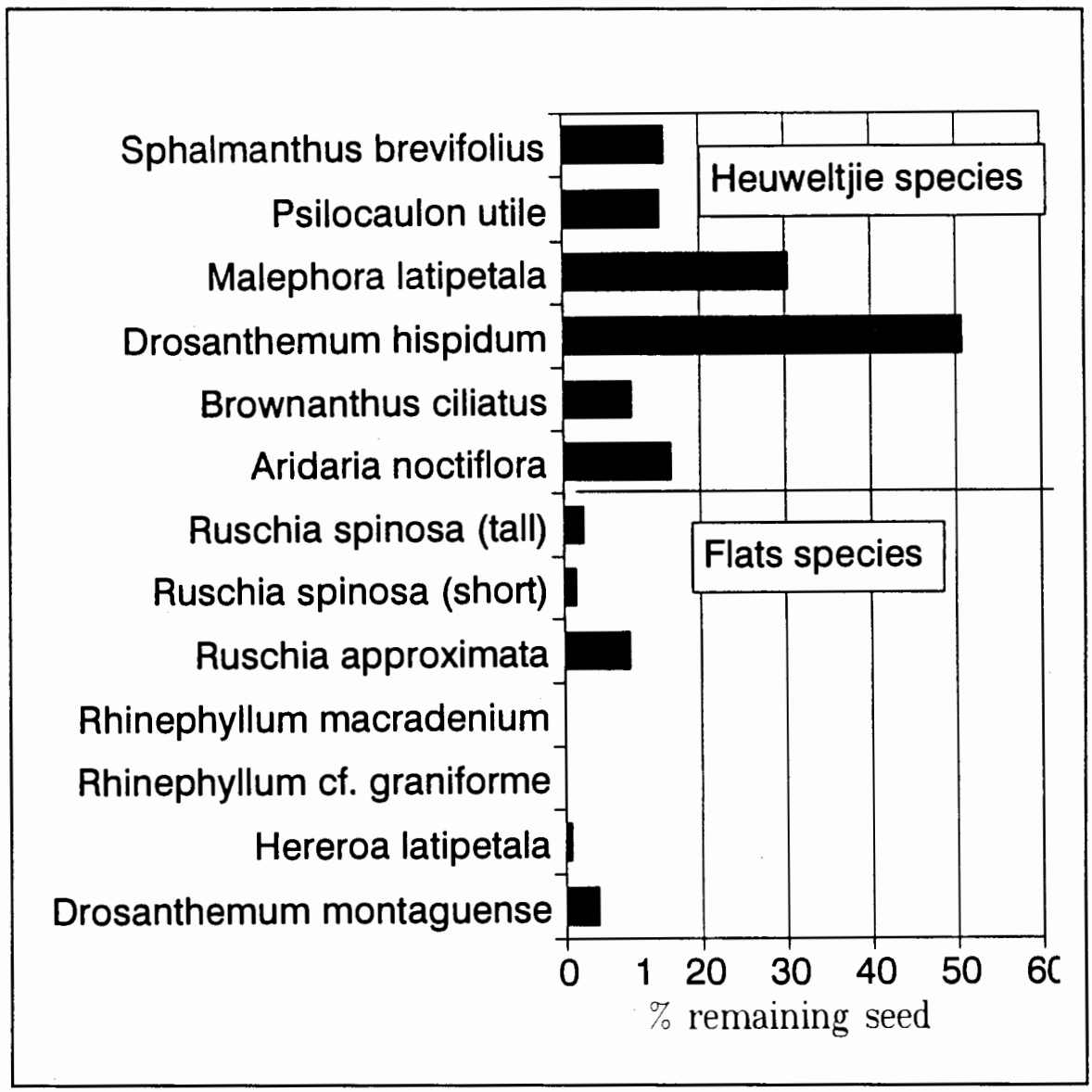

Figure 3-1. Percentage of seed remaining in capsules of six flats species and six heuweltjie species after six months and 177.5 mm of rain. Initial seed numbers were taken from seed counts in capsules collected on December 12 or January 31 (see Table 3-5).

3.6 DISCUSSION

Very clear patterns emerged when comparing the life-history characteristics of species occurring on and off *heuweltjies*.

Species occurring on the flats all had high germination percentages in laboratory trials. Seeds did show some response to temperature. Of the four species that showed significant differences, three had significantly higher germination percentages under a temperature regime which simulated spring/autumn conditions. Seeds of flats species tended to be small, and seeds were released from capsules soon after the first significant rainfall events. Overall germination of *heuweltjie* species was low and did not appear to be controlled by temperature. *Heuweltjie* species tended to retain their seeds in capsules, and seed release was spread out over the year.

The life-history attributes of species occurring on and off *heuweltjies* can be related to disturbance and competition.

Heuweltjies are "hot spots" of disturbance in the succulent karoo landscape. They act as refuges for opportunistic species which are also associated with overgrazed and otherwise disturbed vegetation off *heuweltjies*. Although nutrient levels are higher on *heuweltjies*, this can be discounted when explaining differences in life-history characteristics, since many of the *heuweltjie* species also occur in disturbed sites in the flats where nutrient levels are lower (Milton et al. 1992). Thus, most species which occur on *heuweltjies* are not regarded as *heuweltjie* specialists. For example, Brownanthus ciliatus and Malephora lutea, species normally associated with *heuweltjies* on the study site, are able to dominate adjacent farmlands where the history has been one of heavy grazing (Milton et al. 1992). Acocks (1975) also noted that the dominance of certain "creeping" species of Mesembryanthema, often found on *heuweltjies* in the Little Karoo, appeared to be an "artificial phenomenon, resulting from selective overgrazing and

soil erosion". In contrast with species which normally occur on *heuweltjies*, species which occur on the flats (in undisturbed vegetation) are unable to colonise disturbed areas. It has been noted that many of these longer-lived, woody species disappear in heavily grazed vegetation (Acocks 1975).

Disturbance levels on *heuweltjies* are high and consequently adult population turnover is rapid (B. Bayer, pers. comm., Worcester Veld Reserve, Worcester). The ability of *heuweltjie* species to exploit areas which have been severely overgrazed is associated with their opportunistic life-history characteristics. Species occurring on *heuweltjies* appear to maintain canopy seed banks (higher seed retention than the flats species) as well as soil seed banks (Chapters 4 and 5). The low overall germination of these species indicates some degree of innate dormancy or an after-ripening requirement in the seeds, since germination trials were conducted immediately after collection of fresh seeds. Seeds of *heuweltjie* species have been recorded in soil collected on the flats (Chapter 5), suggesting either that these species are able to disperse off *heuweltjies*, or that seeds may have persisted in the soil from previous disturbance events. These characteristics confer an advantage to *heuweltjie* species when the opportunities for establishment are spatially and temporally variable, and when probability of death after establishment is high. Thus *heuweltjie* species act as pioneers in the successional process proposed by Yeaton and Esler (1990). Long-lived shrubs which occur on the flats are ultimately able to re-invade these areas because the pioneer species provide microhabitats which either trap seeds or shelter seedlings (Chapter 6).

On the flats, the chances of encountering favourable recruitment sites are very low (Yeaton and Esler 1990, Chapter 6), but once seedlings develop into adult plants, they have a higher chance of survival. Flats species are thus geared towards exploiting suitable rain events. All of the flats species release their seeds during the first rain events of the season. They also exhibit rapid germination and low seed dormancy. Seeds of the species occurring on the flats are small and it is generally known that growth rates of seedlings originating from small seeds are

often faster than those in larger seeds (Fenner 1985, Thompson 1987). Jurado and Westoby (1992) investigated seedling growth in relation to seed size in some arid Australian species. They found that seedlings from heavier-seeded species tended to have slower relative growth rates than lighter-seeded species during the first ten days after germination. The "cost" of having competitive life-history characteristics is that many seeds are lost from the system. However, all of the flats species are long-lived perennial shrubs with woody growth forms. This longevity allows adult plants to risk the high probability of seedling mortality. Although seedling mortality rates are very high after germination events (Chapters 6 and 7), some degree of temperature control on seed germination may confer an advantage to seedlings of the flats species, since restricting germination to cooler conditions would reduce the risk of seedling mortality. Germination in the field occurs in autumn when ambient and soil temperatures are declining after the hot summer months and when rainfall is more predictable (Chapters 1 and 7, Henrici 1935).

A few of the general patterns found in this study have been discussed by other authors. A link between plant longevity and germination behaviour of Mesembryanthema has also been noted by Ihlenfeldt (1989). He showed that seeds of long-lived perennials germinated rapidly and had high overall germination (i.e. no dormancy), whereas short-lived species tended to have low overall germination indicating that the seeds were either dormant or had specific germination requirements. This study shows that these patterns are probably related to the habitats of the species. Another general finding in this study was that a strong negative correlation was found between the degree of seed retention and maximum germination in all species. These results are not consistent with findings of Hartmann (1989) who showed that delayed dispersal was correlated with rapid germination and reduced seed dormancy in the genus Agyroderma, whilst rapid seed release was correlated with delayed germination in the genus Oophytum. Hartmann (1989) argued that where capsules represented the main seed bank, there was no need for seeds to be dormant after dispersal.

Unfortunately no information was given on the habitats of these species.

A drawback of using the comparative survey approach to uncover general patterns between the reproductive attributes of species and the habitats in which they occur is that the approach is correlational rather than experimental, and may overlook potentially important confounding factors (Krebbs and Davies 1981), such as phylogenetic constraints. A major problem in this study was that of the species sampled on the flats, none belonged to the sub-family Mesembryanthemoideae. All of the flats species belonged to the sub-family Ruschioideae, so any common responses between these species could in fact be a result of canalised phylogenetic attributes (Krebbs and Davies 1981). The phylogenetic problem was partially resolved because some species of the sub-family Ruschioideae occurred on *heuweltjies*. These species shared similar life-history characteristics with co-occurring Mesembryanthemoideae species (i.e. all had high seed retention and low overall seed germination), suggesting that environmental factors do influence demographic variation to some extent. Generalised linear models which took into consideration both habitat and sub-family indicated that habitat explained more variation in the seed retention and germination data.

A major question remains: why are species in the sub-family Mesembryanthemoideae not represented on the flats in undisturbed environments? In order to answer this question, more needs to be known about the reproductive biology of these species, as well as how they interact with seedlings and adults of different species. One possibility is that the Mesembryanthemoideae are not able to compete successfully with the flats species, as their seeds germinate slowly and exhibit high levels of dormancy. However, the ultimate reason may be linked to plant longevity. All of the species occurring on the flats belong to the sub-family Ruschioideae and are long-lived with woody growth forms. Woodiness is a feature thought to be advanced in the Mesembryanthema (Bittrich and Struck 1989). Perhaps the reason why members of the Mesembryanthemoideae are not represented on the flats is that they are phylogenetically constrained to more

primitive, "herbaceous" growth forms.

Much of the taxonomic work on the Mesembryanthema is based on capsule morphology (Hartmann 1991). The sub-family Mesembryanthemoideae, for example, is characterised by simple, short-lived capsules (< 1 year). These have few of the internal capsule structures which have apparently evolved to retain seeds for longer periods (Hartmann 1988). In contrast, capsules of the sub-family Ruschioideae have a variety of structures which apparently assist in prolonging seed dispersal (Hartmann 1991). It is interesting to note then, that seed retention was greater in species occurring on *heuweltjies*, especially since the majority of these species belonged to the so-called "primitive" Mesembryanthemoideae. The reason for greater seed retention in these species may relate not so much to capsule structure, but to the presence of persistent floral parts which surround the capsules. It was noted, during collection of Aridaria noctiflora and Sphalmanthus brevifolius capsules, that the presence of persistent floral parts may hinder seed dispersal by preventing capsules from opening during rain events.

In conclusion, although an attempt was made to overcome some of the problems associated with the comparative approach in ecology (by considering phylogeny), this approach still has problems. The data interpretation should therefore be treated as plausible hypotheses which require further testing using a more experimental approach. Factorial experiments using seedlings of selected *heuweltjie* and flats species, in which competition and microhabitat availability are manipulated, could provide more answers.

3.7 REFERENCES

Acocks,J.P.H. 1975. Veld types of South Africa. (2nd edition). Memoirs of the Botanical Survey of South Africa 40:1-128.

Armstrong,A.J. and Siegfried,W.R. 1990. Selective use of *heuweltjie* earth mounds by sheep in the Karoo. South African Journal of Ecology 1:77-80.

Baker,R.J. and Nelder,J.A. 1978. The GLIM system. Numerical Algorithms Group, Oxford, England.

Bittrich,V. and Hartmann,H.E.K. 1988. The Aizoaceae- a new approach. Botanical Journal of the Linnean Society 97:239-254.

Bittrich,V and Struck,M. 1989. What is primitive in Mesembryanthemaceae? An analysis of evolutionary polarity of character states. South African Journal of Botany 55:321-331.

Booysen,J. and Rowswell,D.I. 1983. The drought problem in the Karoo areas. Proceedings of the Grassland Society of Southern Africa 18:40-45.

Cohen,D. 1966. Optimising reproduction in a randomly varying environment. Journal of Theoretical Biology 16:1-14.

Cohen,D. 1967. Optimising reproduction in a randomly varying environment when a correlation may exist between the conditions at the time a choice has to be made and the subsequent outcome. Journal of Theoretical Biology 16:1-14.

Cowling,R.M., Esler,K.J., Midgely,G.F. and Honig,M.A. Submit. Plant functional diversity, species diversity and climate in arid and semi-arid southern Africa.

Journal of Arid Environments.

Cowling,R.M., Gibbs Russell,G.E., Hoffman,M.T. and Hilton-Taylor,C. 1989. Patterns of plant species diversity in southern Africa. In: Biotic diversity in southern Africa: concepts and conservation, ed. B.J. Huntley. Oxford University Press, Cape Town. pp 19-50.

Cox,G.W. 1984. The distribution and origin of Mima mound grasslands in San Diego County, California. Ecology 65:1397-1405.

Cox,G.W., Lovegrove, B.G. and Siegfried,W.R. 1987. The small stone content of mima-like mounds in the South African region: implications for mound origin. Catena 14:165-176.

Dean,W.R.J. and Yeaton,R.I. In press. The effects of harvester ant Messor capensis nest-mounds on the physical and chemical properties of soils in the southern Karoo, South Africa. Journal of Arid Environments.

Ellner,S. and Shmida,A. 1981. Why are adaptations for long-range seed dispersal rare in desert plants? Oecologia 51:14-31.

Fenner,M. 1985. Seed Ecology. Chapman Hall. London. 151pp.

Gadgil,M and Solbrig,O.T. 1972. The concept of r- and K- selection: evidence from wild flowers and some theoretical considerations. The American Naturalist 106:14-31.

Garside,S. and Lockyer,S. 1930. Seed dispersal from the hygroscopic fruits of Mesembryanthemum carpanthea (Mesembryanthemum), pomeridiana N.E. Br. Annals of Botany 44:639-655.

Gutterman,Y. 1990. Seed dispersal by rain (ombrohydrochory) in some of the flowering desert plants in the deserts of Israel and the Sinai peninsula. Mitteilungen aus dem Institut für Allgemeine Botanik 23:841-852.

Hartmann,H.E.K. 1988. Fruit types in Mesembryanthema. Beiträge zur Biologie der Pflanzen 63: 313-349.

Hartmann,H.E.K. 1989. Biological adaptation in Mesembryanthema. Excelsa 14:39-44.

Hartmann,H.E.K. 1991. Mesembryanthema. In: Systematics, biology and evolution of some South African taxa, eds. H.P. Linder and A.V. Hall. Contributions to the Bolus Herbarium 13:75-157.

Henrici,M. 1935. Germination of karoo bush seeds. South African Journal of Science 32:223-231.

Hoffman,M.T. 1989. A preliminary investigation of the phenology of subtropical thicket and karroid shrubland in the lower Sundays river valley, S.E. Cape. South African Journal of Botany 55:586-597.

Ihlenfeldt,H.D. 1989. Life strategies of succulent desert plants. Excelsa 14:75-83.

Ihlenfeldt,H.D. 1971. Some aspects of the biology of dissemination of the Mesembryanthemaceae. In: The genera of the Mesembryanthemaceae, ed. H. Herre. Tafelberg, Cape Town. pp 28-34.

Jurado,E. and Westoby,M. 1992. Seedling growth in relation to seed size among species of arid Australia. Journal of Ecology 80:407-416.

Jürgens,N. 1986. Contributions to the ecology of southern African succulent plants. Mitteilungen aus dem Institut für Allgemeine Botanik 21:139-365.

Krebbs,J.R. and Davies,N.B. 1981. An introduction to behavioral ecology. Blackwell Scientific Publications, Oxford. 292pp.

Lockyer,S. 1932. Seed dispersal from hygroscopic Mesembryanthemum fruits; Bergeranthus scapigerus Schw., and Dorotheanthus bellidiformis N.E. Br., with a note on Carpanthea pomeridiana N.E. Br. Annals of Botany 46:323-342.

Lovegrove,B.G. and Siegfried,W.R. 1986. The distribution and formation of mima-like mounds in the western Cape region of South Africa. South African Journal of Science 82:432-436.

Lovegrove,B.G. and Siegfried,W.R. 1989. Spacing and origins of mima-like earth mounds in the Cape. South African Journal of Science 85:108-112.

McCullagh,P. and Nelder,J.A. 1983. Generalised linear models. London, Chapman and Hall. 261pp.

Midgely,G.F. and Musil,C.F. 1990. Substrate effects of zoogenic soil mounds on vegetation composition in the Worcester-Robertson valley, Cape Province. South African Journal of Botany 56:158-166.

Milton,S.J. 1992. Effects of rainfall, competition and grazing on flowering of Osteospermum sinuatum (Asteraceae) in arid Karoo rangeland. Journal of the Grassland Society of South Africa 9:158-164.

Milton,S.J. and Dean,W.R.J. 1990a. Mima-like mounds in the southern and western Cape: are the origins so mysterious? South African Journal of

Science 86:207-208.

Milton,S.J. and Dean,W.R.J. 1990b. Seed production in rangelands of the southern Karoo. South African Journal of Science 86:231-233.

Milton,S.J., Dean,W.R.J. and Kerley,G.I.H. 1992. Tierberg Karoo Research Centre: history, physical environment, flora and fauna. Transactions of the Royal Society of South Africa 48:15-46.

Moore,J.M. and Picker,M.D. 1991. Heuweltjies (earth mounds) in the Clanwilliam district, Cape Province, South Africa: 4 000 year-old termite nests. Oecologia 86:424-432.

Thompson,K. 1987. Seeds and seed banks. New Phytologist 106(supplement): 23-34.

Van Rooyen,M.W., Barkhuizen,A. and Myburgh,S.E. 1980. Saadverspreiding van enkele verteenwoordigers van die Mesembryanthemaceae. South African Journal of Botany 46:173-192.

Van Rooyen,M.W., Theron,G.K. and Grobbelaar,N. 1990. Life form and dispersal spectra of the flora of Namaqualand, South Africa. Journal of Arid Environments 19:133-145.

Werger,M.J.A. 1986. The Karoo and southern Kalahari. In: Hot deserts and arid shrublands vol. B. eds. M. Evenari, I. Noy-Meyer and D.W Goodall. Elsevier, Amsterdam. pp 283-359.

Williams,D.A. 1982. Extra binomial variation in logistic linear models. Applied Statistics 31:144-148.

Yeaton,R.I. and Esler,K.J. 1990. The dynamics of a succulent karoo vegetation: a study of species association and recruitment. Vegetatio 88:103-113.

Zar,J.H. 1984. Biostatistical analysis. Prentice-Hall, New Jersey. 718pp.

CHAPTER 4

SEED BIOLOGY OF THREE SPECIES OF MESEMBRYANTHEMA IN THE SOUTHERN SUCCULENT KAROO

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4.1 ABSTRACT

The seed biology of three Mesembryanthema species, Brownanthus ciliatus (Ait.) Schwant., Rhinephyllum macradenium (L.Bol.) Schwant. and Drosanthemum montaguense L.Bol. was studied at the Tierberg Karoo research centre in the Prince Albert district of the southern Karoo. Variation in capsule and seed numbers was recorded over three sampling periods representing different seed production events. In addition, the soil seed bank was investigated, as well as capsule opening rates and seed germination behaviour. Generally, there was a decline in capsule and seed numbers with time, suggesting that the canopy stored seed bank is limited to the current year's seed production. Large soil seed banks did not appear to be characteristic of the species studied. Estimates of seed production in this study were larger than estimates of other researchers, possibly due to time of data collection. The findings are related to the community structure and dynamics of the vegetation on the study site.

4.2 INTRODUCTION

Members of two subfamilies comprising the Mesembryanthema, viz. Ruschioideae and Mesembryanthemoideae, in the family Aizoaceae (Bittrich and Hartmann 1988) largely dominate the semi-arid Succulent Karoo regions of the southern and southwestern Cape of Southern Africa (Jürgens 1986, Hartmann 1991). Not only do the Mesembryanthema contribute significantly to the exceptionally high diversity of these areas (Cowling et al. 1989), but they also appear to play a vital role in the dynamics of the plant communities in which they occur (Yeaton and Esler 1990). Little work, however, has been done on the population dynamics and ecology of this group (Hartmann 1983). More specifically, basic data on seed banks of Mesembryanthema, and in fact of karoo plants in general, are lacking (Cowling 1986).

Seeds of most Mesembryanthema are stored in hygrochastic capsules (Hartmann 1988). These open during rain when moisture conditions are more favourable for germination and establishment (Garside and Lockyer 1930, Lockyer 1932, Ihlenfeldt 1971, Rawe 1975, Van Rooyen et al. 1980, Gutterman 1990, Hartmann 1991), and close again when dry. The observation that many species retain seeds in their capsules for several seasons as a reserve (Hartmann 1988, 1991), has led to the conclusion that canopy stored seed banks are a widespread phenomenon in the Mesembryanthema (Ihlenfeldt 1971, Hoffman and Cowling 1987).

In this chapter, the seed biology of three species of Mesembryanthema was investigated. In the context of the life histories of the study plants, the findings of this study are related to the community structure and dynamics (Yeaton and Esler 1990) of the vegetation on the study site in the southern Succulent Karoo.

4.3 STUDY SITE AND STUDY SPECIES

The study was conducted over a period of two years (1987-1988) at a moderately grazed site less than 1 km from the Tierberg Karoo Research Centre in the Prince Albert district of the southern Karoo (33°10'S, 22°17'E). The area is situated on a colluvial plain (800 m altitude), 20 km north of the Swartberg mountain range of the Cape Folded Belt. Soils in this area are weakly structured, with lime deposits generally present (Ellis and Lambrechts 1986). The area receives approximately 170 mm of rainfall per year, which falls mostly in autumn and spring. For the period of the study, rainfall records from January 1986 to July 1987 were obtained from the Prince Albert gaol (26 km E of the study site, 830 m altitude, 33°14'S, 22°2'E) (Sue Milton, pers. comm. Fitzpatrick Institute, University of Cape Town) and from August 1987 to December 1988 from the Tierberg research site. These indicated a total rainfall of 204.9 mm in 1986, 134.3 mm in 1987 and 297.0 mm in 1988. The average annual rainfall for 92 years from the Prince Albert gaol is 167 ± 7 mm. Temperatures range from below 0°C to above 30°C with a mean annual temperature of 17.5°C (Milton et al. 1992).

The vegetation on the site is relatively homogeneous, comprising perennial succulent (mostly Mesembryanthema) and non-succulent shrubs. Different plant communities occur along drainage lines and on mima-like mounds or *heuweltjies* (Lovegrove and Siegfried 1989). The study concentrated on two species found on the "flats" vegetation (Milton et al. 1992); Drosanthemum montaguense L.Bol. (sub-family Ruschioideae) and Rhinephyllum macradenium (L.Bol.) Schwant. (sub-family Ruschiodeae); and one species that is often found downslope from *heuweltjies* or in disturbed areas; Brownanthus ciliatus (Ait.) Schwant. (sub-family Mesembryanthemoideae). From now on, the species will be referred to by their generic names. In the succession model proposed in Yeaton and Esler (1990), these species play different roles in the dynamics of the system at the study site. The mound building species of Mesembryanthema are able to colonise open areas between existing vegetation (Brownanthus, Rhinephyllum). These then provide

woody shrubs with protected sites in which to establish (Drosanthemum). (The definition of a woody shrub is based on growth form. Woody shrubs are taller with erect branches and long internodes than the remainder of the species on the study site which are more procumbent in growth form e.g. mound-mesembs). In time, the mound-mesembs are out-competed and replaced by the woody shrub guild. Brownanthus is an ascending, multi-stemmed, non-woody evergreen stem succulent and leaf deciduous species which acts as a primary coloniser in the sequence of species replacements proposed in Yeaton and Esler (1990). This species collects organic matter and soil at its base (mound-mesemb) and thus provides refuges for woody shrubs which appear later on in the successional sequence in this habitat. Rhinephyllum is a procumbent, evergreen and mat-forming species, appearing later on in the successional sequence, thus replacing Brownanthus. Drosanthemum is a semi-deciduous member of the woody shrub guild. This guild relies on the mound-building forms of Mesembryanthema for establishment sites (Yeaton and Esler 1990).

4.4 METHODS

4.4.1 Community structure

Density of the study species per m^2 was calculated from counts of individuals in 10 randomly placed 5 x 5 m quadrats. For each of the study species, plant diameter and height was recorded for calculation of cover. For a more detailed description of the community structure of the site, see Yeaton and Esler (1990) and Milton et al. (1992). Three line transects, each 50 m, long were used to count the number of dead versus living individuals of each species.

4.4.2 Canopy-stored seeds

For each species, all seed capsules from ten (April 1987) or fifteen (February and December 1988) randomly selected plants were harvested. Plants of Brownanthus were sub-sampled (i.e. capsules from half of the plant were harvested), as large numbers of seed capsules made collection too time consuming. For each plant, the length along the long axis (L) and the greatest width at right angles to the length (W) were measured. These measurements were used in the calculation of plant size using the formula $\pi LW/4$. All three species flower in spring (September), and the resulting capsules mature to release their seed from December to March of the following year. Seed capsules collected in April 1987 were from the previous year's seed production (1986); those collected in February 1988 were from 1987 seed production; and those collected in December 1988 were from 1988 seed production. The capsules were sorted into current and previous season's production (based on observation; older capsules from the previous season's production had weathered more than the current year's capsules) and counted. The number of seeds per capsule was determined from 30 randomly selected capsules. The seeds were retained for germination trials.

4.4.3 Soil-stored seeds

To investigate the soil-stored seed bank, soil samples were collected from the study site during winter (July 1989) and summer (January 1990). Thirty soil samples were taken at each sampling time from 15 x 23 cm randomly located quadrats (equivalent to the area of an incubation seed tray), and to a depth of 2 cm. Each soil sample was mixed and placed in a 2 cm layer over a standard soil mixture. These were then placed in randomised blocks in a nursery at the Worcester Veld Reserve (33°39'S, 19°26'E). Trays were kept moist using an automated spray system, and seedling recruitment was monitored over an entire year for both sample periods (i.e. from July 1989 to July 1990 for the winter

samples, and from January 1990 to January 1991 for the summer samples).

4.4.4 Capsule opening times

Rate of capsule opening was measured by dripping water onto capsules of each species in the field (capsules were kept constantly moist), and recording the length of time before the capsule was fully opened. This was carried out under different temperatures and relative humidities by examining the opening times at different periods during the day.

4.4.5 Seed germination

Seeds collected for the determination of the current year's seed production were used in the laboratory germination trials. Twenty five seeds were sown in each of four petri dishes (Diameter = 9 mm) containing three layers of Schleicher & Schuell filter paper saturated with a 0.75 $g.l^{-1}$ solution of Benlate fungicide (to prevent fungal infection). Petri dishes were then placed in clear plastic bags in controlled environmental conditions within two electrocool growth cabinets (photon flux density: 49 μmol $m^{-2}s^{-1}$). The two cabinets were set at alternating temperature/light cycles designed to simulate the average day and night temperatures in summer (30°C, 14 hr light period and 15°C, 10 hr dark period) and winter (20°C, 14 hr light period and 10°C, 10 hr dark period). Seeds were considered germinated when the radicle had emerged and elongated to 2 mm. Numbers of germinated seeds were recorded at two day intervals for a month after initiation of the germination trials.

4.5 RESULTS

4.5.1 Community structure

Brownanthus had the greatest number of adult plants and the highest percentage cover of the three species. Averaged data for the ten, 5 x 5 m quadrats gave an overall canopy spread cover (m^2, x ± S.D.) of 2.5 ± 2.09 for Brownanthus, 1.17 ± 0.07 for Rhinephyllum and 1.70 ± 2.29 for Drosanthemum. Adult plant densities (numbers of individuals) per m^2 were 0.37 ± 0.32 for Brownanthus, 0.30 ± 0.19 for Rhinephyllum and 0.16 ± 0.18 for Drosanthemum. The mean density figures were used in the seed bank calculations. A count of the dead versus living individuals along three, 50 m long line transects indicated that 24% of the Brownanthus plants, 22% of the Rhinephyllum plants, and 8% of the Drosanthemum plants encountered were dead.

4.5.2 Canopy-stored seeds

Overall, Brownanthus produced more seed capsules per plant (Table 4-1) and per m^2 (Table 4-2) than Drosanthemum or Rhinephyllum. The capsule numbers (per m^2) for the latter two species were within the same order of magnitude, although there was some variation between years (Table 4-2). Plant sizes were calculated to be (x ± S.D., n = 30) 1564.09 ± 882.23 cm^2 for Drosanthemum; 1027.17 ± 830.39 for Brownanthus and 765.27 ± 650.73 for Rhinephyllum. For all three species, at each sampling period, the current year's capsules (0 year capsules) were more numerous than the previous year's capsules, and hence contributed more significantly to overall capsule numbers. Generally, there was a decline in capsule numbers with time (i.e. comparing this year's capsule production with last year's production) (Tables 4-1, 4-2). One way analyses of variance of capsule numbers per plant over each sampling period for each species and for each

capsule age (significance between species), indicated that there was little variation in overall seed capsule numbers between years, except for the current year's capsule numbers of Drosanthemum (ANOVA: F-ratio = 4.73, $P < 0.05$, d.f. = 2, 36), and the 1 year capsule numbers of Rhinephyllum (ANOVA: F-ratio = 14.46, $P < 0.01$, d.f. = 2, 35). The below average rainfall in 1987 (see study site description) may explain the low numbers of seed capsules produced by Drosanthemum in its 1987 production year (i.e. seed collected in February 1988) (Tables 4-1, 4-2). Brownanthus and Rhinephyllum appeared not to be affected by this variation in rainfall, as similar numbers of capsules were produced each year (Table 4-1).

There was a great deal of variation in numbers of seed counted per capsule, probably due to collection times (Table 4-3). The highest seed numbers per capsule (Table 4-3) were recorded in December 1988 for current year's capsules. These data are probably closest to the actual numbers of seeds produced per capsule, as little rain had fallen between the time of production and collection. Lower numbers of seeds recorded for April 1987 and February 1988 indicate that seeds had possibly been released already. Of the three species, Rhinephyllum produced the most seeds per capsule, more than 5.7 times as much as Brownanthus and 3.5 times as much as Drosanthemum (Table 4-3, using December 1988 0 yr data). This corresponds with the capsule sizes (diameter in mm, n = 10) of ($x \pm$ S.D.) 8.35 ± 0.98 for Rhinephyllum, 4.75 ± 0.40 for Drosanthemum and 3.82 ± 0.36 for Brownanthus.

Although Rhinephyllum produced fewer capsules per m^2 than Brownanthus (Table 4-2), it produced more seeds per capsule and thus effectively was capable of producing approximately as many seeds per m^2 as Brownanthus (February 1988 data, Table 4-4). Drosanthemum, on the other hand, produced far fewer seeds per m^2 (Table 4-4).

4.5.3 Soil-stored seeds

No seedlings were recorded from the winter collected soil samples. However, 46 Brownanthus seedlings, 5 Rhinephyllum seedlings, and 26 Drosanthemum seedlings were recorded in the summer collected soil samples. From the soil samples, seedling density was calculated to be 44.4 seedlings per m^2 for Brownanthus; 4.8 seedlings per m^2 for Rhinephyllum; and 25.0 seedlings per m^2 for Drosanthemum. These figures are 67, 420 and 22 times smaller than the numbers of seeds produced per m^2 for each species respectively (Table 4-4, December 1988 data).

4.5.4 Capsule opening times

There was a significant difference between capsule opening times of the different species and between opening times of the same species at different temperatures (Table 4-5). Brownanthus showed the most rapid opening of all the species under the different temperatures and humidities. Drosanthemum had the next most rapidly opening capsules and Rhinephyllum the slowest (Table 4-5). Brownanthus and Rhinephyllum appeared to have an optimum temperature for opening (± 24°C). Temperatures on either side of this showed slower opening times. In Drosanthemum, capsules opened faster as temperatures increased (Table 4-5).

4.5.5 Seed germination

Brownanthus showed the lowest level of germination with only 12% of the (plump) seeds germinating after 30 days (December 1988, Table 4-6) (non-plump seeds were not viable). Better germination results were obtained using the winter simulated temperature regime of a 10°C night and a 20°C day. Germination trials were conducted immediately after collecting seeds, this may indicate some degree of innate dormancy in Brownanthus, however it may also be that conditions for germination were not provided in the experiment (i.e. enforced dormancy). Higher

overall germination percentages were obtained for Drosanthemum and Rhinephyllum, although there was a great deal of variation between sampling times and between temperature treatments (Table 4-6). Chi-square tests for Drosanthemum ($\chi^2 = 37.3$; $P \leq 0.0001$) and Rhinephyllum ($\chi^2 = 6.26$; $P \leq 0.04$) indicated significant temperature and sampling time effects. We were unable to perform a chi-square test on Brownanthus data due to very small values in the data set.

Table 4-1. Variation in capsule numbers per plant (x ± S.D., n = 15 plants for February and December 1988, n = 10 plants for April 1987) for Drosanthemum montaguense, Brownanthus ciliatus and Rhinephyllum macradenium at three sampling times. One way analyses of variance were conducted on the data, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, N.S. = non significant.

Sampling time	Drosanthemum	Brownanthus	Rhinephyllum	Significance between spp.
a) Current year's capsules per plant (0 yr)				
Apr 87	186.11 ± 135.50	299.67 ± 140.20	78.00 ± 22.40	*
Feb 88	49.07 ± 70.55	193.47 ± 316.50	73.47 ± 59.03	N.S.
Dec 88	101.87 ± 103.98	403.67 ± 323.97	58.53 ± 32.19	***
Significance within spp.	*	N.S.	N.S.	
b) Previous year's capsules per plant (1 yr)				
Apr 87	55.10 ± 31.88	68.29 ± 80.50	28.00 ± 12.72	N.S.
Feb 88	45.27 ± 52.86	89.07 ± 141.21	18.40 ± 17.17	N.S.
Dec 88	35.20 ± 40.91	21.27 ± 51.89	110.47 ± 73.66	***
Significance within spp.	N.S.	N.S.	**	
c) Total number of capsules per plant (0 yr + 1 yr)				
Apr 87	272.50 ± 167.39	384.89 ± 230.74	111.20 ± 30.44	N.S.
Feb 88	94.33 ± 104.18	282.53 ± 403.34	91.87 ± 71.09	N.S.
Dec 88	137.07 ± 117.22	424.93 ± 329.57	169.00 ± 99.85	**
Significance within spp.	**	N.S.	N.S.	

Table 4-2. Variation in capsule numbers per m^2 ($x \pm$ S.D., n = 15 plants for February and December 1988, n = 10 plants for April 1987) for Drosanthemum montaguense, Brownanthus ciliatus and Rhinephyllum macradenium at three sampling times. Results are calculated from number of capsules per plant multiplied by density of individuals per m^2. Density figures are as follows ($x \pm$ S.D.): Drosanthemum = 0.16 ± 0.18 plants/m^2; Brownanthus = 0.37 ± 0.32 plants/m^2 and Rhinephyllum = 0.30 ± 0.19 plants/m^2. One way analyses of variance were conducted on the data, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, N.S. = non-significant.

Sampling time	Drosanthemum	Brownanthus	Rhinephyllum	Significance between spp.
a) Current year's capsules per m^2 (0 yr)				
Apr 87	29.78 ± 23.00	110.89 ± 55.03	23.40 ± 6.70	**
Feb 88	7.97 ± 11.30	71.60 ± 117.10	22.00 ± 17.70	*
Dec 88	16.30 ± 16.60	149.40 ± 119.90	17.60 ± 9.70	***
Significance within spp.	*	N.S.	N.S.	
b) Previous year's capsules per m^2 (1 yr)				
Apr 87	8.80 ± 5.10	25.27 ± 32.17	8.40 ± 4.08	N.S.
Feb 88	7.20 ± 8.50	32.95 ± 52.20	5.50 ± 5.20	*
Dec 88	5.60 ± 6.50	7.90 ± 19.20	33.10 ± 22.10	***
Significance within spp.	N.S.	N.S.	**	
c) Total number of capsules per m^2 (0 yr + 1 yr)				
Apr 87	43.60 ± 26.78	142.41 ± 85.38	33.36 ± 9.13	**
Feb 88	15.09 ± 16.67	90.41 ± 129.07	27.56 ± 21.33	*
Dec 88	21.93 ± 18.76	157.23 ± 121.94	50.95 ± 29.95	***
Significance within spp.	**	N.S.	N.S.	

Table 4-3. Variation in numbers of seeds per capsule (x ± S.D., n = 30 capsules) for Drosanthemum montaguense, Brownanthus ciliatus and Rhinephyllum macradenium at three sampling times. One way analyses of variance were conducted on all of the data except for the within species significance tests in (b), where two sample t-tests were used, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, N.S. = non-significant. - = missing data.

Sampling time	Drosanthemum	Brownanthus	Rhinephyllum	Significance between spp.
a) No. seed in current year's capsules (0 yr)				
Apr 87	7.77 ± 3.80	11.97 ± 10.81	12.77 ± 17.68	N.S.
Feb 88	39.27 ± 28.57	11.73 ± 10.22	56.03 ± 80.21	**
Dec 88	32.97 ± 33.20	19.87 ± 7.13	113.93 ± 64.40	***
Significance within spp.	***	**	***	
b) No. seed in previous year's capsules (1 yr)				
Apr 87	-	-	-	
Feb 88	13.84 ± 13.15	5.80 ± 5.68	0.10 ± 0.30	***
Dec 88	3.17 ± 6.85	0.00 ± 0.00	0.13 ± 0.34	**
Significance within spp.	**	***	N.S.	

Table 4-4. Variation in numbers of seeds per m^2 for Drosanthemum montaguense, Brownanthus ciliatus and Rhinephyllum macradenium at three sampling times. Results are calculated by multiplying mean numbers of capsules per m^2 (Table 4-2) by mean numbers of seeds per capsule (Table 4-3).
- = missing data. > sign used for (c) April 87 data due to missing data of 1 yr capsules.

Sampling time	Drosanthemum	Brownanthus	Rhinephyllum
a) Seeds per m^2 in current year capsules (0 yr)			
Apr 87	231	1327	299
Feb 88	310	840	1233
Dec 88	537	2969	2005
b) Seeds per m^2 in previous years capsules per (1 yr)			
Apr 87	-	-	-
Feb 88	100	191	0.6
Dec 88	18	0	4
c) Total number of seeds per m^2 (0 yr + 1 yr)			
Apr 87	>231	>1327	>299
Feb 88	410	1031	1234
Dec 88	555	2969	2009

Table 4-5. Mean capsule opening times in seconds (x ± S.D, n = 10) for Drosanthemum montaguense, Brownanthus ciliatus and Rhinephyllum macradenium at different temperatures and relative humidities. Kruskal-Wallis analyses of variance (Zar 1984) were used for significance testing, *** = $p < 0.001$

Temp. (°C)	Rel.Humid. (%)	Drosanthemum	Brownanthus	Rhinephyllum	Sig. between spp.
34	51	106 ± 28	98 ± 35	196 ± 25	***
29	52	121 ± 25	56 ± 12	240 ± 38	***
24	50	120 ± 28	45 ± 90	176 ± 26	***
13	15	191 ± 32	65 ± 60	244 ± 20	***
Sig. within spp.		***	***	***	

Table 4-6. Percentage germination of seed from current years (0 yr) capsules for Drosanthemum montaguense, Brownanthus ciliatus and Rhinephyllum macradenium at two temperature regimes: 10°C night / 20°C day and 15°C night / 30°C day and three sampling times. Germination recorded after 30 days, n = 100 seeds.

Sampling time	Drosanthemum		Brownanthus		Rhinephyllum	
	10/20	15/30	10/20	15/30	10/20	15/30
Apr 87	60	26	8	2	77	50
Feb 88	12	46	6	2	58	60
Dec 88	22	40	12	2	38	48

4.6 DISCUSSION

The estimates of seed production per m^2 in this study were far higher than those provided by Milton and Dean (1990) for the same species at an equivalent moderately grazed site at Tierberg. They estimated a total of 236 seeds per m^2 for Brownanthus, 122 seeds per m^2 for Drosanthemum and 19 seeds per m^2 for Rhinephyllum with 7, 20 and 9 seeds counted per capsule for each species respectively. It is possible that they did not take into consideration the time of capsule collection, since this greatly influences seed counts due to seed release after rainfall, as indicated by the variation in our data. Estimates of numbers of seeds produced per m^2 in this study are comparable to those of selected perennial species in the Sonoran and Great Basin deserts (Kemp 1989).

For all three species, the current year's seed production contributed significantly to overall canopy seed numbers. One year old capsules contained fewer seeds suggesting that the canopy stored seed bank is fairly limited to the current year's seed production (Table 4-3). This is also indicated in Table 4-4 which shows the very high numbers of seeds per m^2 for 0 year capsules as opposed to 1 year capsules. Data (in Chapter 3) for 1989's seed production of Mesembryanthema on the Tierberg study site gives some indication of the low seed retention capabilities of the three species. Six months after seed production (and after 177.5 mm of rainfall), Drosanthemum had 3.9% of its seed remaining, whilst Brownanthus had 8.0% of it's seed remaining. None of the Rhinephyllum seeds remained in the capsules (n = 25 seed capsules counted per species). Canopy-stored seed banks (and soil seed banks) do not appear to be characteristic of the perennial species that were studied. The seed source for these species in favourable recruitment years is likely to be from seeds produced in that year.

The seed biology data appear to corroborate the cyclic succession ideas proposed in Yeaton and Esler (1990). The three species of Mesembryanthema chosen for this study occupy different stages in the proposed successional sequence (see

above). Brownanthus was proposed as a primary coloniser in the successional sequence. This species had the highest reproductive output in terms of capsule numbers per individual and per m^2 and its overall seed production was high. Since Brownanthus is out-competed by later successional species (Yeaton and Esler 1990), and since its adult plant turnover is possibly faster than the other species (the largest percentage of dead plants was recorded for this species), more emphasis is likely to be placed on seed bank persistence. The soil seed data indicated however, that seedlings only germinated from soil collected in summer (January)(at the onset of seed dispersal), whilst winter-collected soil cores (July) produced no seedlings (even though the cores were monitored over the entire seasonal range). A larger data set did show some germination for Brownanthus from winter collected soil cores (Chapter 5), so it is possible that a small seed bank exists for this species, although it was not indicated in this data set, possibly due to under sampling. Poor germination of Brownanthus in laboratory experiments pointed to seed dormancy, this makes it difficult to conclude whether the seed bank of this species is persistent or transient using our techniques. The question of seed banks for this species can only be satisfactorily answered by measuring viability of seed extracted from the soil.

Although Rhinephyllum produced as many seed per m^2 as Brownanthus, this species did not appear to have a persistent seed bank. Seeds were rapidly released from the canopy and the high germination percentages excluded the possibility of a soil seed bank. The fact that no seed germinated from the winter collected soil cores, confirmed this. This species appears to use a "broadcast-spawning" approach, with an emphasis on seed dispersal and numbers. Most of it's seed is probably lost during the peak germination period corresponding to the April rains (Chapter 6). Rhinephyllum occurs later in the proposed successional sequence, where the chances of encountering favourable establishment sites are lower. The slow capsule opening rate of this species provides some protection against dispersal into sub-optimal rainfall conditions.

The lowest reproductive output was recorded for Drosanthemum. As a semi-deciduous, woody shrub appearing much later on in the successional sequence, this species appeared to follow a strategy of adult plant persistence. Only 8% of the adult plants recorded were dead. Drought is the recurrent disturbance factor in the Succulent Karoo which is most likely to result in seedling and adult plant mortality. Drosanthemum is semi-deciduous and woody and therefore physiologically better equipped to deal with extended droughts than the other two species (N. Phillips pers. comm., Department of Botany, University of Cape Town).

In conclusion, the reproductive biology of the three species studied appeared to reflect differences in the degree to which seed banks are a part of the plants' strategy of promoting population survival within the successional framework described in Yeaton and Esler (1990).

4.7 REFERENCES

Bittrich,V. and Hartmann,H.E.K. 1988. The Aizoaceae - a new approach. Botanical Journal of the Linnean Society 97:239-254.

Cowling,R.M. 1986. A description of the Karoo Biome Project. South African National Scientific Programmes Report no. 122, Council for Scientific and Industrial Research, Pretoria. 42pp.

Cowling,R.M., Gibbs Russell,G.E., Hoffman,M.T. and Hilton-Taylor,C. 1989. Patterns of plant species diversity in Southern Africa. In: Biotic diversity in southern Africa: concepts and conservation, ed. B.J. Huntley. Oxford University Press, Cape Town. pp 19-50.

Ellis,F. and Lambrechts,J.N. 1986. Soils. In: The Karoo biome : a preliminary synthesis. Part 1 - physical environment, eds. R.M. Cowling, P.W. Roux and A.J.H. Pieterse. South African National Scientific Programmes Report no. 124, Council for Scientific and Industrial Research, Pretoria. pp 18-38.

Garside,S. and Lockyer,S. 1930. Seed dispersal from the hygroscopic fruits of Mesembryanthemum carpanthea (Mesembryanthemum), pomeridiana N.E. Br. Annals of Botany 44:639-655.

Gutterman,Y. 1990. Seed dispersal by rain (ombrohydrochory) in some of the flowering desert plants in the deserts of Israel and the Sinai peninsula. Mitteilungen aus dem Institut für Allgemeine Botanik 23:841-852.

Hartmann,H.E.K. 1983. Interaction of ecology, taxonomy and distribution in some Mesembryanthemaceae. Bothalia 14:653-659.

Hartmann,H.E.K. 1988. Fruit types in Mesembryanthema. Beiträge zur Biologie

der Pflanzen 63:313-349.

Hartmann,H.E.K. 1991. Mesembryanthema. In Systematics, biology and evolution of some South African taxa, eds. P. Goldblatt, H.E.K. Hartmann, E.G.H. Oliver, H.P.Linder and B.E. van Wyk. Contributions to the Bolus Herbarium 13:75-157.

Hoffman,M.T. and Cowling,R.M. 1987. Plant physiognomy, phenology and demography. In: The Karoo biome : a preliminary synthesis. Part 2 - vegetation and history, eds R.M Cowling and P.W. Roux, South African National Scientific Programmes Report no. 142, Council for Scientific and Industrial Research, Pretoria. pp 1-34.

Ihlenfeldt,H.D. 1971. Some aspects of the biology of dissemination of the Mesembryanthemaceae. In: The genera of the Mesembryanthemaceae, ed. H. Herre. Tafelberg, Cape Town. pp 28-34.

Jürgens,N. 1986. Contributions to the ecology of southern African succulent plants. Mitteilungen aus dem Institut für Allgemeine Botanik 21:139-365.

Kemp,P.R. 1989. Seed banks and vegetation processes in deserts. In: Ecology of soil seed banks, eds. M.A. Leck, V.T Parker and R.L. Simpson. Academic Press, New York. pp 257-281.

Lockyer,S. 1932. Seed dispersal from hygroscopic Mesembryanthemum fruits; Bergeranthus scapigerus Schw., and Dorotheanthus bellidiformis N.E. Br., with a note on Carpanthea pomeridiana N.E. Br. Annals of Botany 46:323-342.

Lovegrove,B.G. and Siegfried,W.R. 1989. Spacing and origins of mima-like earth mounds in the Cape. South African Journal of Science 85:108-112.

Milton,S.J. and Dean,W.R.J. 1990. Seed production in rangelands of the southern Karoo. South African Journal of Science 86:231-233.

Milton,S.J., Dean,W.R.J. and Kerley,G.I.H. 1992. Tierberg Karoo Research Centre: history, physical environment, flora and fauna. Transactions of the Royal Society of South Africa 48:15-46.

Rawe,R. 1975. Mesembryanthemaceae : seed dispersal and capsule behaviour. Excelsa 5:105-107.

Van Rooyen,M.W., Barkhuizen,A. and Myburgh,S.E. 1980. Saadverspreiding van enkele verteenwoordigers van die Mesembryanthemaceae. South African Journal of Botany 46: 173-192.

Yeaton,R.I. and Esler,K.J. 1990. The dynamics of a succulent karoo vegetation: a study of species association and recruitment. Vegetatio 88:103-113.

Zar,J.H. 1984. Biostatistical analysis. Prentice-Hall, New Jersey. 718pp.

CHAPTER 5

DYNAMICS OF SOIL-STORED SEED BANKS IN SEMI-ARID, SUCCULENT KAROO VEGETATION

5.1 ABSTRACT

Soil seed bank dynamics were monitored on the farm Tierberg in the Succulent Karoo of southern Africa. Soil was collected from three distinct microhabitats (from open areas between shrubs, and from under Ruschia spinosa and Brownanthus ciliatus adult plants) over summer and winter to determine spatial and seasonal variation in seed banks. Seed decay was measured by placing seed bags in the field and by recording remaining viable seeds over two years. Most arid-zone seed bank studies have concentrated in areas with an abundance of annuals and the general conclusion is that seed banks are persistent and large, with annual species as the main contributors. Little is known about perennial seed banks, and at Tierberg, annuals are not common. The observed seed bank densities at Tierberg were low compared with other studies and distinctly seasonal (71-426 seeds/m^2 in summer vs 17-90 seeds/m^2 in winter). Larger seed banks and more species were recorded in summer shortly after peak seed production and dispersal. The seasonal variability, combined with evidence of rapid seed deterioration, indicates the transient nature of most species in the seed bank. In favourable recruitment years, seedlings are likely to be from seeds produced in the previous flowering season. Microhabitat differences (with respect to the number of seeds) were as apparent during periods of high soil seed density as they were during periods of low soil seed density. Seeds were more abundant under shrubs than in open areas and seed distribution patterns were largely a result of dispersal differences among individual species. Seed densities did not correlate well with adult plant densities.

5.2 INTRODUCTION

Seed bank studies are an important consideration in the development of a predictive understanding of plant community structure and function (Roberts 1981, Leck et al. 1989). In arid and semi-arid environments, where germination and recruitment are the critical stages in the life cycles of most plants, seed banks are thought to play a major role in population dynamics. Seed bank studies in arid environments have been concentrated mainly in areas with an abundance of annuals (Nelson and Chew 1977, Van Rooyen and Grobbelaar 1982, Parmenter and MacMahon 1983, Reichman 1984, Price and Reichman 1987, Henderson et al. 1988, Coffin and Lauenroth 1989). These studies indicate that seed banks in arid areas are often persistent and large (Von Willert et al. 1992) with annual species as the main contributors. There is often a poor correspondence between the occurrence (and relative abundance) of species in the seed bank and of those in the adult plant community (Moore 1980, Coffin and Lauenroth 1989), although this is not always the case (Henderson et al. 1988). Where differences do occur, the seed bank usually contains early successional species, often annuals, which rely on seed banks as part of their opportunistic life history strategies (Moore 1980). What happens when annuals are absent from a system? Knowledge of seed banks of perennial species in arid environments is very poor (Leck et al. 1989).

In the southern Karoo, part of a large semi-arid rangeland covering approximately 33% of South Africa's land surface (Rutherford and Westfall 1986), plant communities are comprised of relatively stable, long-lived perennials. Annuals comprise less than 1% of the biomass and cover at any time (Milton et al. 1992). In a model of the dynamics of this system, several mound-building shrubs of the Mesembryanthema have been identified as early successional species (Yeaton and Esler 1990). These act as nurse plants for a later successional woody shrub guild. The turnover in this system is very slow (McAuliffe 1988, Yeaton and Esler 1990). To what extent the species in this system rely on soil seed banks is unknown. For

example, do the mound-building pioneer species have larger seed banks than those which establish later on in the successional sequence? and, can spatial patterns in the seed banks be explained in terms of the succession model? Although some data exist for established seedlings (Yeaton and Esler 1990), more detailed information is required on the seed bank and recruitment stages in the life cycles of the key species in the system. This information would enable an understanding of the processes involved in the dynamics of the system.

Soil seed bank dynamics were monitored (the word "seed" is used in the broad sense to include fruits as well as true seeds) on the farm Tierberg in the Succulent Karoo of southern Africa (Milton et al. 1992). The study addressed the following questions: *(1) What is the size of the soil-stored seed bank? (2) Is there is any evidence for seasonality in seed bank size? (Seasonal fluctuations in seed bank size would provide some indication of the permanence of the seed bank at Tierberg.) (3) How long do seeds remain viable in or on the soil (i.e. how persistent or transient are the seed banks)? (4) What is the relationship between soil-stored seed and microhabitat? And finally, (5) does seed bank composition reflect the abundance of species in the existing plant community?*

For the purpose of this study, a transient seed bank is defined as one in which component seeds do not remain viable longer than one year (Thompson and Grime 1979).

5.3 METHODS

5.3.1 Study site and study species

The research was conducted on the plains of the Tierberg Karoo Research Centre (Milton et al. 1992) near Prince Albert in the Succulent Karoo (33°10'S, 22°17'E). Vegetation on the plains (or "flats" in Yeaton and Esler (1990)) is relatively

homogeneous, comprising perennial succulent (mostly Mesembryanthema, family Aizoaceae) and non-succulent (mostly Asteraceae) shrubs. The plains occupy approximately 78% of the 100 ha study site (Milton et al. 1992), the rest of the area being occupied by mima-like mounds or *heuweltjies* (Lovegrove and Siegfried 1986) and drainage lines. The study site receives approximately 170 mm of rain per annum, falling mostly in late summer/autumn (February-May) and spring (September to November) (Milton et al. 1992). Flowering occurs during the spring although some species show an opportunistic response to rain events (Hoffman 1989, Milton 1992). The heaviest rains occur between February and May, thus coinciding with seed dispersal and germination (Chapter 6). Temperatures at the study site range from -5°C (winter minimum) to 43°C (summer maximum) with a mean annual temperature of 17.5°C (Milton et al. 1992).

Work was conducted at both a community and a species level in this study. Species selected to answer more specific questions were those highlighted in Yeaton and Esler (1990), viz. Pteronia pallens L.f., Ruschia spinosa Hartm. & Stuber. (L.Bol.) L. Bol., Brownanthus ciliatus (Ait.) Schwant. and Galenia fruticosa (L.f.) Sond. The characteristics of these species are provided in Table 5-1. These species play different roles in the dynamics of the system (Yeaton and Esler 1990). Brownanthus ciliatus is a mound-building, leaf succulent which is able to colonise open areas. This species is replaced by Ruschia spinosa (referred to as Eberlanzia cf. vulnerans in Yeaton and Esler 1990) in more mature vegetation. Both species collect organic matter and soil at their bases (mound-mesemb), and thus provide refuges for woody shrubs which appear later on in the successional sequence in this habitat. Pteronia pallens is a woody shrub which establishes in mound-mesembs, although litter is also a favoured germination site (Chapter 6). Galenia fruticosa is a very common woody shrub in the area. The role that this species plays in the succession has not been studied.

5.3.2 Estimation of germinable seed banks

To estimate seed bank densities, a seedling emergence technique was used (Thompson and Grime 1979, Roberts 1981, Gross 1990). This method provides an estimate of the number of viable, germinable seeds in the soil. The drawback of the technique is that it may underestimate viable, dormant seed abundances (Roberts 1981, Gross 1990). An attempt to avoid this problem was made by monitoring seedling emergence from the same soil samples over a year and therefore covering an entire seasonal range of temperatures. In addition, specific field tests were done on the longevity of seeds in the soil (section 5.3.3). The advantage of the technique is that it is the most practical for community level studies. It is the least tedious and time consuming of the estimation methods, especially when dealing with large sample sizes (Roberts 1981, Gross 1990). Soil quadrats representing samples of the soil-stored seed bank were collected from within a 200 x 200 m area in the Tierberg study site during summer (January) and winter (July) of 1989 and 1990. In terms of rainfall totals, 1989 and 1990 were similar years. In the six months prior to sample collection times, the rainfall totals were 103 mm (January 1989), 103 mm (January 1990), 145 mm (July 1989) and 154.8 mm (July 1990) (Milton et al. 1992). On each occasion, fifty soil samples were collected from each of three microhabitats identified as important sites for germination and establishment (Yeaton and Esler 1990). These sites were open areas between shrubs, and under Ruschia spinosa (Mesembryanthema) and Brownanthus ciliatus (Mesembryanthema) adult plants. Samples were collected from 15 x 23 cm quadrats (equivalent to the area of the incubation seed trays), and to a depth of 2 cm. Seed densities in the soil profile decline greatly below a depth of 2 cm in arid environments (Nelson and Chew 1977, Reichman 1984). It was assumed that this was the case for seed banks sampled in this study. Each sample contained 690 cm^3 of soil, yielding a total volume for each microhabitat at each sampling time of 34 500 cm^3. This volume is well within (and often larger than) the range of volumes used in most seed bank studies in arid environments (e.g. Parmenter and MacMahon 1983, Hassan and West 1986, Henderson et al.

1988). Each soil sample was mixed and placed in a 2 cm layer overlying a standard sterile soil mixture contained in 15 x 23 x 8 cm seed trays. The trays were placed in randomised blocks (and moved randomly every two weeks) initially in a nursery at the Worcester Botanical Gardens (33°36'S, 19°27'E), and then later (from January 1989) under similar conditions in a nursery at the Worcester Veld Reserve (33°39'S, 19°26'E). The nurseries were 3 km apart. The mean minimum and maximum temperatures monitored at Tierberg and at the Worcester Veld Reserve over the study period were similar (Milton et al. 1992 and unpublished data, Weather Bureau, Pretoria). Trays were exposed to rain and filtered sun, and were kept moist during dry periods using an automated light spray system. For each set of samples, seedling emergence was monitored at two week intervals over the entire seasonal range (i.e. from January to January of the following year, or from July to July of the following year). Once counted and identified, seedlings were carefully removed so as not to disturb the soil surface.

5.3.3 Seed decay

Fresh seeds were collected from Pteronia pallens, Ruschia spinosa, Brownanthus ciliatus and Galenia fruticosa (Table 5-1). Plump seeds (filled with endosperm) were hand sorted and placed in nylon mesh bags (10 cm x 10 cm). For each species, bags containing 25 seeds each, were located on the soil surface and 2 cm below the soil surface in each of the following microhabitats during March 1989; in open areas between shrubs, under Ruschia spinosa adult plants and under Pteronia pallens adult plants. These microhabitats were chosen because open areas between shrubs are favourable microhabitats for germination and recruitment of the Mesembryanthema species, whilst adult Mesembryanthema species like Ruschia spinosa provide sheltered microhabitats for the recruitment of woody shrubs like Pteronia pallens (Yeaton and Esler 1990).

Four replicate bags for each species were retrieved from the field during September 1989, March 1990, September 1990 and March 1991. These times correspond

to the peak rainfall periods in the area (Milton et al. 1992). Seeds remaining in the excavated bags were then transferred to each of four petri dishes (diameter 9 mm) containing three layers of Schleicher & Schuell filter paper saturated with a 0.75 $g.l^{-1}$ solution of Benlate fungicide. Petri dishes were then placed in clear plastic bags in controlled environmental conditions within an electrocool growth cabinet (photon flux density 49 μmol $m^{-2}s^{-1}$). In exploratory germination trials, average germination percentages tended to be higher for spring/autumn simulated temperature regimes (Table 5-2). Van Rooyen and Grobbelaar (1982) also found that lower temperatures were more suitable for germination of succulent karoo species. The growth cabinet was therefore set at an alternating temperature/light cycle designed to simulate an average spring/autumn day and night temperature of a 20°C, 14 hr light period and a 10°C, 10 hr dark period. Seeds were considered germinated when the radicle had emerged and elongated to 2 mm. Numbers of germinated seeds were recorded at two day intervals for a month after the initiation of the germination trials. Viability of the seed that did not germinate was determined by cutting up the seeds and checking if endosperm still existed in the seed (plump seeds). Unfortunately, seeds were too small for tetrazolium tests. The number of viable seeds was the sum of the germinated and plump seeds.

In order to determine if overall percentage germination changed with seed age regardless of field conditions, seeds collected from the same cohort used in the seed burial experiment were stored (for up to two years) in brown paper bags and tested in laboratory germination trials under the same conditions described above. These control germination trials were conducted at the same time as trials conducted on seeds retrieved from the field (i.e. during September 1989, March 1990, September 1990 and March 1991).

5.3.4 Vegetation cover

In order to compare seed bank estimates with adult plant cover, cover data provided by Yeaton and Esler (1990) was used (since the same study area was

used). The particular area of the study site used in this study was dominated by Pteronia pallens. The majority of the plants on the study site are long-lived perennials. It was therefore assumed that the proportional representation of adult plants on the study site would remain constant during the two years of the study (Beatley 1980).

5.3.5 Statistical Analysis

Generalised linear models (statistical package: GLIM, Baker and Nelder 1978) were used on the seed bank and seed decay data. This method avoids the assumptions of normality associated with many statistical procedures (Zar 1984). Log-linear models were fitted to the seed bank (count) data using Poisson error distributions and log link functions. Logit-linear models were fitted to the seed decay data using binomial error distributions and logit link functions (McCullagh and Nelder 1983). Final models were selected using partial and marginal effects and with the use of the Akaike (1974) criterion. Soil seed abundances are heterogeneous due to a variety of factors including differential dispersal patterns (Major and Pyott 1966). Where variation in the data was more than that described by Poisson distributions, a scale factor (over-dispersion parameter) was introduced. In the case of extra binomial variation, the Williams (1982) procedure was used. In order to obtain a measurement of the percentage variation (P) in the data explained by the final model, the deviance (Dev) of the selected model was compared with the deviance of the model which contained only the mean using:

$$P = 100 \times (Dev(\text{mean only}) - Dev(\text{model}))/Dev(\text{mean only})$$

where Dev(-) is the residual deviance (McCullagh and Nelder 1983).

Statgraphics 5.0 (STSC Inc.) was used for two sample t-tests on arcsin transformed percentage germination data. In order to determine whether the numbers of seeds observed in the seed bank study occurred in similar frequency to a) adult plant numbers and b) seed production of the more common species occurring on the study site, Chi-squared tests on observed versus expected seed

data were conducted using the GLIM package.

Sorensen's similarity indices (Smith 1986) were used to measure the correspondence between species composition of the seed bank (over four sampling periods) and of the adult vegetation. Sorenson's index = (2 x C)/(S1 + S2), where C = the number of species common to both adult vegetation and seed bank flora, and S1 and S2 are total numbers of species in both floras.

5.4 RESULTS

5.4.1 Spatial and temporal patterns of seed abundance

The total number of seedlings emerging (from n = 50 seed trays) from soil collected in different seasons (and watered over an entire year) varied up to 11 fold in open sites, 6 fold under Ruschia spinosa plants and 9 fold under Brownanthus ciliatus plants, with the majority of seedlings being recorded in the summer months (Table 5-3a). The effects of season, site and year were estimated using a generalised linear model with a Poisson error distribution and a log link function. A scale factor of 11.99 was used, indicating considerable over-dispersion, possibly due to the clumping of seeds. Apart from significant site, season and year effects, there was also a season-by-year interactive effect. The final model explained 96.8% of the variation in the data (Appendix 5.7a).

In order to cope with considerable variation in the seedling counts, the data was examined in terms of mean number of seedlings per soil sample. A log-linear model was fitted to these data using a Poisson error distribution and a log link function (Table 5-3b, Appendix 5.7b). The final model explained 94% of the variation in the data. The model, which included season and site effects only (Pearsons Chi-squared for the model = 3.206; d.f. = 8; $0.95 > P > 0.9$), indicated that there was no year effect on average seedling abundances between 1989 and 1990. The

model implied that average seedling abundances (and by inference seed bank sizes) depend on site and season. These two factors act independently (i.e. there were no interactions). Using the parameter estimates generated by GLIM, the expected average number of seedlings that would germinate from soil collected in three microhabitats over two seasons was calculated (Table 5-4a). These results indicated a seasonal decrease of 80% in the average numbers of seedlings germinated from soils collected in summer to soils collected in winter. This finding held for all sites. The effect of a site shift from open to under Ruschia spinosa (both in summer and in winter) was to raise the expected number of seedlings by 39% and the effect of the site shift from open to under Brownanthus (both in summer and winter) was to raise the expected number by 340%. These findings held for both seasons. It must be stressed that one would expect to find extremely large variation about these mean values in field situations. In the above model, averages were used instead of totals. The model using totals required the use of a large scale factor, implying considerable variation in the data.

Cumulative seedling emergence curves indicated that seeds in soils collected in summer germinated rapidly, and by July (approximately 20 weeks later), no more germination had occurred (Fig. 5-1). Germination in the soils collected in winter was slower and more widely spread over the year. Seedlings were still germinating in January, after 28 weeks of watering. There was a slight pulse of seedlings in the winter 1989 soil samples when the trays were moved to the Worcester Veld Reserve in January 1990. A model (GLIM) of the time (weeks) taken to reach 50% germination indicated a significant site, season and year effect, as well as an interaction between year and site (Pearsons Chi-squared for the model = 3.81; d.f. = 5; $0.75 > P > 0.5$). The final model explained 96% of the variation in the data (Appendix 5.7c).

Species richness (i.e. the number of seedling species emerging from the soil samples, Table 5-3c) varied up to 2.7 fold over the four sampling periods and three microhabitats, with more species being recorded in the summer months. A

log-linear model was fitted to these data. The final model (Pearsons Chi-squared for the model = 5.042; d.f. = 8; 0.90 > P > 0.75) indicated that differences in species counts between seasons and between sites were significant, but that there was no year effect. The model explained 75% of the variation (Appendix 5.7d). The expected number of seedling species found in the three sites from summer- and winter-collected soils (Table 5-4b) indicated that a season shift from summer to winter (in all sites) would lower the number of species found by 66%. A site shift from open to under Ruschia spinosa adults raised the expected number of seedling species by 40%, and a site shift from open to under Brownanthus raised the expected number of seedling species by 64%.

Within the seed banks, the distribution patterns of seeds varied considerably among individual species (Appendix 5.9). Winged seeds (e.g. Osteospermum sinuatum and Tetragonia spicata) and seeds with a pappus (e.g. Pteronia pallens) were never recorded in open sites. Seedlings of these species were recorded under Brown-anthus ciliatus and to a lesser extent, under Ruschia spinosa adults. B. ciliatus seed abundances were highest under B. ciliatus adults. This implies that dispersal distances are short and that seeds aggregate about mother plants. For all of the selected species, which were also the most common species as adults, more seed-lings were recorded in summer (Appendix 5.9).

5.4.2 Seed decay

Total germination of Ruschia spinosa seeds (Table 5-5) did not change over two years of storage under laboratory conditions (Model: $\text{Log}(\pi/1-\pi) = \mu$, where π is the probability of seeds germinating; Pearsons Chi-squared = 9.1; d.f. = 19; 0.98 > P > 0.95). Seeds of Galenia fruticosa did not germinate at all under laboratory conditions. An aging effect was, however, recorded for laboratory stored seeds of Pteronia pallens:
(Model: $\text{Log}(\pi/1-\pi) = \mu + \beta^{\text{time}}$; Pearsons Chi-squared = 19.07; d.f. = 15; 0.25 > P > 0.1)

and Brownanthus ciliatus:

(Model: $\text{Log}(\pi/1-\pi) = \mu + \beta^{time}$; Pearsons Chi-squared = 20.82; d.f. = 15; $0.25 > P > 0.1$).

Seed decayed rapidly under field conditions. Logit-linear models were fitted to the data (as above), and due to considerable extra-binomial variation, Williams' (1982) procedure was applied. In all cases there were significant time and site (open versus under Ruschia spinosa versus under Brownanthus ciliatus) effects (Appendix 5.7e). All species, except Ruschia spinosa showed a significant burial (surface versus 2 cm) effect (Table 5-6, Appendix 5.7e). Although significant site differences were found, these were not easy to interpret due to considerable variation in responses. For simplicity, the site data was combined to form two treatment categories: buried seed and surface seed (Table 5-6). It was not possible to distinguish between the causes of seed deterioration (i.e. failed germination or seed decay) in this experiment, although predation was excluded. Survival was lowest for Pteronia pallens seeds (Table 5-6). The only species that had a significant proportion of seeds remaining in the seed bags was Galenia fruticosa (Table 5-6). Tables 5-7 and 5-8 were generated from the seed decay data and are discussed under section 5.5.

5.4.3 Seed versus adult plant abundance

A total of 40 species were identified in the seed bank of this community, 38 of which occurred on or near the site as adults (Appendix 5.8). Of the 186 species recorded as adult plants on the 100 ha study site (Milton et al. 1992), 44 (25%) occurred on the plains where the study was conducted. Twenty of these species (46%) were recorded in the seed bank study (combined total over all seasons and microhabitats). The bulk of the species on the study site occur on *heuweltjies* (56 species), washes (78 species) and in drainage lines (84 species) (note that some species are scored more than once if they are found in two or more of these habitats). Seventeen (30%), nineteen (24%) and thirteen (16%) of these species

were recorded in the seed bank study respectively, despite the fact that *heuweltjies*, washes and drainage lines were avoided during sampling. Thirty (54%) of the species recorded in the seed bank were common or abundant as adults (Milton et al. 1992); but only sixteen (29%) of these were species which are common or abundant on the plains (Appendix 5.8 and Milton et al. 1992). The species composition of the seed bank (totalled over the four sampling periods and three microhabitats) in comparison with the total adult flora of the study site (186 species) gave a Sorenson's index of 33.6. This is high when one considers that only the plains of the study site were sampled. A consideration of the plains flora only, gave a Sorensons coefficient of 41.7. Generally, a close correspondence was not found between the species composition of the seed bank, and that of the plant community at all sampling times and within each microhabitat (Tables 5-9 and 5-10). Higher similarities were found when we considered the plains flora only, but these values were not very different to coefficients calculated using the entire flora (Table 5-9).

Species with plant covers of less than 1% were proportionally far better represented in the seed bank than some of the more abundant species (Appendix 5.9). Observed versus expected seedling numbers (with respect to relative frequencies of adult plants) differed markedly in all sampling periods (Table 5-10). Pteronia spp. were distinctly under-represented in the seed bank, despite being dominants in the adult vegetation and despite sampling biased towards this species. Ruschia spinosa seeds were more abundant in the seed bank (Appendix 5.9), although still under-represented with respect to the adult plants (Table 5-10)(χ^2 = 62.2; d.f. = 3; $P < 0.0001$). Galenia fruticosa was proportionally over-represented in the seed bank (χ^2 = 556.8; d.f. = 3; $P < 0.0001$), as was Brownanthus ciliatus (χ^2 = 4492.9; d.f. = 3; $P < 0.0001$)(Table 5-10). The relationship between seed bank sizes and seed production was also studied, using data provided by Milton and Dean (1990)(Table 5-10). Observed versus expected seedling numbers (with respect to relative frequencies of seed production) were markedly different in all sampling periods (Table 5-10), although some of the

differences were not as extreme as the comparison with adult plant frequencies (e.g. Pteronia spp.) (Table 5-10). With respect to seed production, Galenia fruticosa was proportion-ally under-represented in the seed bank (χ^2 = 573.9; d.f. = 3; P < 0.0001), whilst Ruschia spinosa (χ^2 = 1220.5; d.f. = 3; P < 0.0001) and Brownanthus ciliatus (χ^2 = 5982.8; d.f. = 3; P < 0.0001) were over-represented. A cautionary note must be sounded when interpreting these data, since relative seed production may vary from year to year (Chapter 4).

Table 5-1. Characteristics of four karoo shrubs from the Tierberg Karoo Research Centre, Cape Province, South Africa.

Species	Pteronia pallens	Ruschia spinosa	Brownanthus ciliatus	Galenia fruticosa
Family	Asteraceae	Aizoaceae Mesembryanthema	Aizoaceae Mesembryanthema	Aizoaceae
Seed production (per m^2)[1]	60	107	170	2208
Dispersal mode	wind	water	water	wind/passive
Structural attributes	evergreen, woody, non-succulent	evergreen, woody, leaf-succulent	leaf-deciduous non-woody, stem- and leaf-succulent	semi-deciduous woody non-succulent
Stage in succession[2]	3	2	1	1?

[1]Data from Milton and Dean (1990)
[2]from Yeaton and Esler (1990): 1 = early successional, 3 = late successional.

Table 5-2. Percentage germination (after 30 days) of freshly collected seed of five species from the Tierberg Karoo Research Centre, Cape Province, South Africa. Seeds were germinated at two temperature regimes: 10°C night / 20°C day and 15°C night / 30°C day, simulating spring/autumn and summer conditions respectively. Data are means ± standard deviations, n = 5 petri dishes of 25 seed each, except Brownanthus ciliatus where n = 4 petri dishes of 25 seed each. Two sample t-tests were used for significance testing on arcsin transformed data; * = $P < 0.05$; N.S. = non-significant.

Species	Percentage germination			
	10/20	15/30	t	Sig.
Pteronia pallens	85.6 ± 10.4	72.0 ± 10.2	2.10	N.S.
Ruschia spinosa	86.4 ± 8.3	72.0 ± 8.5	2.67	*
Brownanthus ciliatus	5.0 ± 2.0	0.0 ± 0.0	-	-
Galenia fruticosa	0.0 ± 0.0	0.0 ± 0.0	-	-

Table 5-3. a) Total number of seedlings, b) average number of seedlings (mean ± standard deviation) c) number of seedling species recorded from 50, 690cm^2 soil samples collected over two years (1989, 1990), two seasons (summer, winter) and three microhabitats (open, and under Ruschia spinosa and Brownanthus ciliatus adult plants from the Tierberg Karoo Research Centre, Cape Province, South Africa.

a) Total number of seedlings:			
	Microhabitat		
Season	Open	Under Ruschia	Under Brownanthus
Summer 1989	121	252	606
Winter 1989	31	101	149
Summer 1990	284	247	735
Winter 1990	27	40	86
b) Average number of seedlings: (per sample)			
Summer 1989	2.4 ± 2.5	5.1 ± 4.4	12.1 ± 9.8
Winter 1989	0.6 ± 0.9	2.1 ± 2.0	3.1 ± 2.5
Summer 1990	5.7 ± 9.6	4.9 ± 4.0	14.7 ± 12.0
Winter 1990	0.6 ± 1.3	0.9 ± 1.4	1.7 ± 1.9
c) Species numbers:			
Summer 1989	16	18	27
Winter 1989	12	13	18
Summer 1990	10	23	23
Winter 1990	10	13	11

Table 5-4. Generalised log-linear model estimates of a) the expected average number of seedlings that would germinate from soil collected in three microhabitats over two seasons and b) the expected average number of seedling species that would germinate from soil collected in three microhabitats over two seasons.

a) Seedling numbers		
Microhabitat	**Season**	
	Summer	Winter
Open	3.88	0.78
Under Ruschia spinosa	5.40	1.08
Under Brownanthus ciliatus	13.20	2.65
b) Species numbers		
Open	14.67	9.52
Under Ruschia spinosa	20.20	13.29
Under Brownanthus ciliatus	23.81	15.67

Table 5-5. Germination of laboratory stored seeds of Pteronia pallens, Ruschia spinosa, Brownanthus ciliatus and Galenia fruticosa from the Tierberg Karoo Research Centre, Cape Province, South Africa. Seeds were tested from 0 to 24 months after storage at room temperatures in the laboratory. Data are means ± standard deviations, n = 4 petri dishes, each containing 25 seeds.

Species	Months after seed collection				
	0	6	12	18	24
P. pallens	20.8 ± 2.5	16.8 ± 2.1	16.0 ± 2.1	12.5 ± 7.6	8.0 ± 1.4
R. spinosa	21.5 ± 2.4	24.5 ± 0.6	20.8 ± 3.0	21.3 ± 4.1	25.0 ± 0.0
B. Ciliatus	6.3 ± 3.4	1.0 ± 1.4	4.0 ± 1.6	2.5 ± 1.7	2.0 ± 1.4
G. fruticosa	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0

Table 5-6. Survival of seeds of four karoo species from the Tierberg Karoo Research Centre, Cape Province, after 6, 12, 18 and 24 months of field exposure. Seeds were buried at 2 cm or placed on the soil surface. Data are mean percentages of plump seeds per bag ± S.D.; 25 seeds per bag; n = 12 bags.

	Months of field exposure			
	6	12	18	24
Ruschia spinosa				
Surface	25.7 ± 16.1	12.0 ± 13.0	2.3 ± 4.0	0.00 ± 0.00
Buried	14.7 ± 14.1	11.3 ± 15.3	5.7 ± 6.5	7.3 ± 7.4
Galenia fruticosa				
Surface	62.3 ± 11.8	57.7 ± 8.1	51.0 ± 14.8	43.7 ± 13.7
Buried	78.0 ± 19.3	64.0 ± 9.4	61.7 ± 12.4	50.0 ± 16.0
Brownanthus ciliatus				
Surface	33.3 ± 34.5	26.7 ± 24.0	14.7 ± 18.0	2.0 ± 4.7
Buried	24.3 ± 18.1	15.0 ± 9.2	9.3 ± 5.8	5.0 ± 8.0
Pteronia pallens				
Surface	22.0 ± 21.6	3.0 ± 9.2	0.00 ± 0.00	0.00 ± 0.00
Buried	16.0 ± 20.0	0.7 ± 2.3	0.00 ± 0.00	0.00 ± 0.00

Table 5-7. Probabilities of seed survival in the soil (means of buried and surface survival probabilities) of four species at the Tierberg Karoo Research Centre, Cape Province, South Africa.

Species	Months of field exposure			
	6	12	18	24
Pteronia pallens	0.19	0.09	0.00	0.00
Ruschia spinosa	0.20	0.62	0.35	0.00
Brownanthus ciliatus	0.29	0.71	0.59	0.34
Galenia fruticosa	0.70	0.87	0.92	0.83

Table 5-8. Predicted and actual numbers of seeds per m^2. Predicted seed numbers were calculated assuming constant annual seed inputs (using actual data provided by Milton and Dean 1990, see Table 5-1) and using the average probabilities of seed survival in the soil (from the seed decay data). Equilibrium seed bank densities were calculated under two scenarios a) no post-dispersal predation and b) post-dispersal predation rates of 32.5% (Milton and Dean 1990). The range given is immediately after seed dispersal and six months later.

Species	Number of seeds per m^2		
	Predicted		Recorded
	a) No predation	b) Predation	
Pteronia pallens	71.4-1.0	23.2-0.3	7.0-0.2
Ruschia spinosa	133.0-13.3	43.2-4.3	31.2-3.2
Brownanthus ciliatus	240.0-42.0	78.0-13.7	82.3-9.3
Galenia fruticosa	4990.7-2371.5	1622.0-770.7	74.1-6.8

Table 5-9. Sorensons coefficients of similarity by year, season and microhabitat of the species composition of the seed bank versus the species composition of a) the entire adult flora and b) the adult species found on the plains of the study site at the Tierberg Karoo Research Centre, Cape Province, South Africa.

Season	Microhabitat			
	Open	Under Ruschia	Under Brownanthus	Total
a) Entire adult flora				
Summer 1989	14.2	15.9	23.9	27.4
Winter 1989	10.6	11.5	15.9	17.7
Summer 1990	8.8	19.5	20.4	24.8
Winter 1990	8.8	11.5	9.7	15.0
b) Adult species found on plains of study site				
Summer 1989	20.8	25.0	27.1	31.0
Winter 1989	12.5	14.6	22.9	22.9
Summer 1990	14.6	29.2	33.3	37.5
Winter 1990	12.5	14.6	16.7	20.8

Table 5-10. Comparison between observed (obs) seed frequencies (totalled over three microhabitats, see Table 5-5) and expected (exp) seed frequencies calculated from a) the relative frequency of adult plants (data from Yeaton and Esler 1990) and b) the relative frequency of seeds produced (data from Milton and Dean 1990) on the Tierberg Karoo Research Centre, Cape Province, South Africa. Chi-squared goodness of fit tests were used on the data. *** = $P < 0.001$.

a)		Observed and expected seed numbers							
Species	**Adult relative frequency**	**Summer 1989**		**Winter 1989**		**Summer 1990**		**Winter 1990**	
		Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp
Pteronia spp.	0.323	37	239.3	1	57.2	4	346.6	13	33.3
Ruschia spinosa	0.257	141	190.4	40	45.5	164	275.8	17	26.5
Galenia fruticosa	0.121	135	89.7	36	21.4	390	129.8	7	12.5
Brownanthus ciliatus	0.066	350	48.9	90	11.7	433	70.8	49	6.8
Rhinephyllum macradenium	0.061	4	45.2	0	10.8	8	65.5	10	6.3
Osteospermum sinuatum	0.049	3	36.3	0	8.7	4	52.6	2	5.1
Drosanthemum montaguense	0.044	3	32.6	1	7.8	2	47.2	0	4.5
Hereroa spp.	0.040	17	29.6	2	7.1	19	42.9	2	4.1
Ruschia approximata	0.031	0	23	0	5.5	2	33.3	0	3.2
Ruschia dolomitica	0.008	9	5.9	0	1.4	12	8.6	0	0.8
Tetragonia spicata	0.002	42	1.5	7	0.0	35	0.3	3	0.2
		n = 741		n = 177		n = 1073		n = 103	
		$\chi^2 = 3293.2$		$\chi^2 = 751.5$		$\chi^2 = 3443.2$		$\chi^2 = 331.7$	
		d.f. = 10		d.f. = 10		d.f. = 10		d.f. = 10	
		***		***		***		***	

b)		Observed and expected seed numbers							
Species	**Seed production relative frequency**	**Summer 1989**		**Winter 1989**		**Summer 1990**		**Winter 1990**	
		Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp
Pteronia spp.	0.068	37	46.9	1	11.6	4	69.8	13	6.8
Ruschia spinosa	0.036	141	24.8	40	6.1	164	36.9	17	3.6
Galenia fruticosa	0.746	135	507.8	36	125.1	390	755.1	7	73.6
Brownanthus ciliatus	0.056	350	38.6	90	9.5	433	57.5	49	5.6
Rhinephyllum macradenium	0.004	4	2.8	0	0.7	8	4.1	10	0.4
Osteospermum sinuatum	0.022	3	15.2	0	3.7	4	22.6	2	2.2
Drosanthemum montaguense	0.025	3	17.3	1	4.3	2	25.7	0	2.5
Hereroa spp.	0.006	17	4.1	2	1.0	19	6.2	2	0.6
Ruschia approximata	0.047	0	32.4	0	8.0	2	48.2	0	4.7
		n = 690		n = 170		n = 1026		n = 100	
		$\chi^2 = 3419.0$		$\chi^2 = 958.4$		$\chi^2 = 3249.8$		$\chi^2 = 694.0$	
		d.f. = 8		d.f. = 8		d.f. = 8		d.f. = 8	
		***		***		***		***	

Table 5-11. Seed bank sizes (number of seeds per m^{-2}) from soil collected from three microhabitats in summer and winter on the Tierberg Karoo Research Centre, Cape Province, South Africa. Data are means ± standard deviations; n = 50.

Season	Microhabitat		
	Open	Under Ruschia	Under Brownanthus
Summer 1989	70.74 ± 73.92	147.27 ± 126.11	351.94 ± 285.26
Winter 1989	17.97 ± 27.57	61.46 ± 59.14	90.45 ± 71.90
Summer 1990	164.67 ± 277.72	142.63 ± 116.25	426.15 ± 346.43
Winter 1990	16.81 ± 37.98	24.93 ± 40.59	49.86 ± 54.79

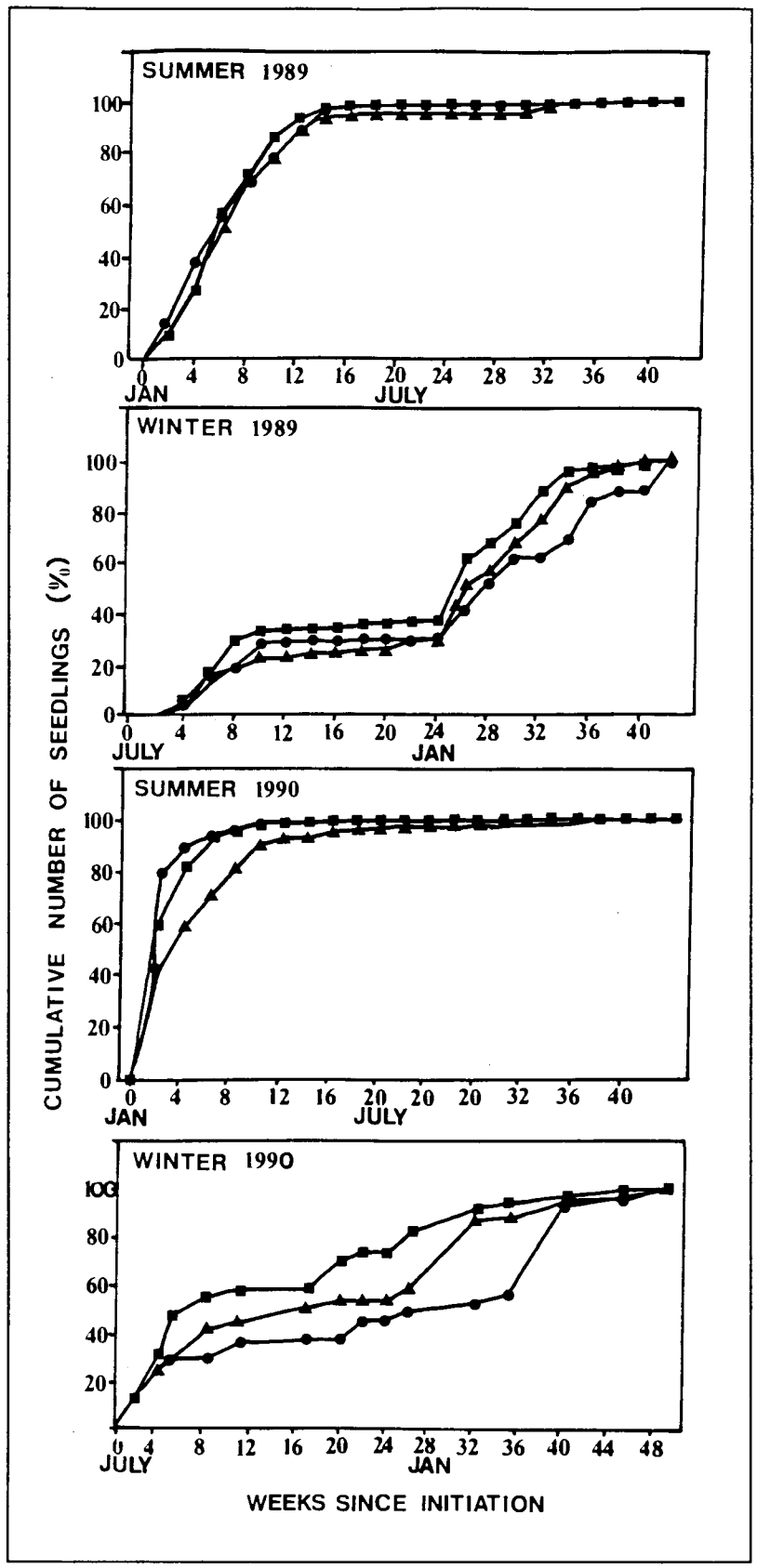

Figure 5-1. Cumulative seedling emergence curves summed over n = 50, 690 cm^3 soil samples collected over two years (1989, 1990), two seasons (summer, winter) and three microhabitats (open●, under Ruschia spinosa▲ and under Brownanthus ciliatus■ adult plants).

5.5 DISCUSSION

What is the size of the soil stored seed bank? Is there any evidence for seasonality in seed bank size? How long do seeds remain in or on the soil?

From the field seed decay data, the mean survival probabilities of seeds in the soil were calculated (Table 5-7). These values, along with estimates of annual seed input per m^2 (Milton and Dean 1990) were used in a simple transition matrix to generate rough predictions of seed bank sizes immediately after seed dispersal, and six months later (Table 5-8). It was assumed that there were constant annual seed inputs and a) no post-dispersal seed predation or b) post-dispersal predation levels of 32% (Milton and Dean 1990). Given the calculated ranges of seed bank sizes, it was expected that seasonal variation in seed banks would be considerable (Table 5-8). Despite the short-comings of the seedling emergence technique (Roberts 1981, Gross 1990), the data did indicate seasonality in seed bank sizes. The size of the soil seed bank in mature karoo vegetation varied considerably between seasons (Table 5-9). Larger seed banks and more seedling species were recorded in the summer months shortly after the peak seed production and dispersal period. This seasonal variability, combined with the evidence of rapid seed deterioration of most species in field situations, indicates the transient nature of most species in the seed bank (Roberts 1986, Coffin and Lauenroth 1989). This is probably due to the variable inputs (seed production, dispersal) and depletions (granivory, germination, decay) which control seed bank size (Reichman 1984).

Very few data are available for comparison of seed banks of perennial communities in different semi-arid and arid regions of the world. Most work has been done in desert regions with a significant proportion of annual species for which considerably larger seed banks have been recorded. For example, Nelson and Chew (1977), working in the annual-rich Mojave desert, reported mean numbers of seeds per m^2 ranging between 269 to 6 151 in open areas to between 3 578 to 37 259 seeds per m^2 under shrub canopies. Reichman (1984) reported seed densities of 10 000 to 15 000 seeds per m^2 near shrubs as opposed to 4 000 to 5 000 in open

areas in the Sonoran desert. North American Great Basin desert communities are characterised by plant associations dominated by perennial shrubs with few annuals (Turner 1982). Reports of peak seed bank densities from these shrub steppe desert communities range from 137 seeds per m^2 under shrubs and 45 seeds per m^2 in open areas (Hassan and West 1986) to 3 940 seeds per m^2 (microhabitats were not specified) (Parmenter and MacMahon 1983). Seed densities in the annual-rich Succulent Karoo in Namaqualand, southern Africa, ranged from 5 000 to 41 000 seeds per m^2 (Van Rooyen and Grobbelaar 1982). The seed bank estimates in this study were considerably lower (17 to 426 seeds per m^2, Table 5-11). The maximum number of soil-stored seeds recorded in this study was 426.2 ± 346.4 per m^2 (Table 5-11). This figure is very low compared with most arid systems (Brown et al. 1979). It has been estimated that perennial shrubs on the plains of the study site produce approximately 3 000 seeds per m^2 (Milton and Dean 1990). This is also low when compared with North American seed production estimates (Pulliam and Brand 1975, Hobbs and Mooney 1986). A considerable number of seeds produced on the study site are lost from the system as a result of granivory. 32% of the estimated annual seed production (Milton and Dean 1990) is removed by the Harvester ant Messor capensis (Dean and Yeaton 1992). Except for Galenia fruticosa, the recorded numbers of seeds per m^2 were generally within the predicted range, when post-dispersal predation rates of 32% were assumed (although this probably not a uniform figure for all species). The low seed production and soil-stored seed estimates reflect the fact that the majority of the species on the study site are perennials. Similar seed bank patterns are found in other, very different vegetation types, for example the North American wetlands (Leck 1989).

From the seed decay data it was predicted that Galenia fruticosa would have the largest seed banks, followed by Brownanthus ciliatus, Ruschia spinosa and Pteronia pallens. Predicted seed bank sizes were generally low, even when assuming no post-dispersal seed predation (Table 5-8). Brownanthus ciliatus seeds were the most abundant, but sampling was biased in favour of this species. It is surprising that Galenia fruticosa does not completely dominate the vegetation, as this species

accounts for 72% of the total seed production on the study site (Milton and Dean 1990). This species maintains a seed bank and its seeds remain viable for several years in the field. In laboratory germination trials this species does not germinate at all unless the seed coat is scarified (unpublished data). Large numbers of Galenia fruticosa seedlings have been recorded after recruitment events (Chapter 6). The role of Galenia fruticosa in the overall dynamics of the system is not well understood in these studies; it's role may only be revealed by long term studies.

In general, the dominant flats species in the Tierberg Karoo area appear to depend very little on canopy (Chapter 4) or soil seed banks for regeneration. The strategy of most perennials in this environment is probably to produce a small number of seeds every year. Most of these seeds appear not to persist in the seed bank, possibly because of seed decay or losses to granivory and germination. The seed source in favourable recruitment years is therefore likely to be from seeds produced during the previous flowering season. Although a significant year effect was not detected in this study (similar rainfall amounts were recorded in both sampling years), the transient seed bank sizes may be affected by low rainfall events prior to seed production (Chapter 4).

Are the soil-stored seed banks microhabitat specific?

Microhabitat differences in the soil-stored seed banks were apparent both during periods of high (summer) and low (winter) soil seed density. Variations in soil seed abundances, both within microhabitats (reflected in the standard deviations) and between microhabitats, were considerable (Table 5-11), reflecting the spatial heterogeneity of the seed banks. Average seed densities were higher under shrubs than in open spaces between shrubs. This is consistent with findings in North American deserts (Nelson and Chew 1977, Reichman 1984).

It would appear that the microhabitat differences in seed bank densities are largely a result of variation in dispersal among individual species. Wind-blown seeds, for

example, were more commonly associated with adult plant cover, whilst water-dispersed Mesembryanthema seeds were found in all microhabitats sampled. Sampling was biased in favour of those species under which we sampled (Brownanthus ciliatus, Ruschia spinosa). Even when seedlings of these species were excluded from the analysis, shrub-covered sites were still important as seed traps. These species may also provide sheltered microhabitats into which many less tolerant seedling species (especially woody species) can recruit (Yeaton and Esler 1990, Chapter 7). Osteospermum sinuatum and Tetragonia spicata are both highly palatable, with large cotyledons and leaves, so establishment beneath canopies of non-palatable shrubs (Mesembryanthema) possibly provides them with an added advantage against herbivory and/or water stress. Seedlings of Osteo-spermum sinuatum and Pteronia pallens are more vulnerable to water stress than those of Ruschia spinosa (Chapter 7). However, the dispersal differences between species raises the possibility that seedlings found in supposedly more favourable microhabitats may not be nursed, but rather "trapped". This challenges the view in the dynamics model (Yeaton and Esler 1990) that seedling recruitment of some species is facilitated by the presence of others (see Chapter 6)

Does seed bank composition reflect the abundance of species in the existing plant community?

Soil seed densities did not appear to correlate well with adult plant densities. This is consistent with findings in other arid systems (Kemp 1989). This discrepancy may be partially explained by the highly patchy distribution of seeds in the landscape, owing to non-uniform dispersal or merely to short dispersal distances combined with the patchy distribution of adult plants (Yeaton and Esler 1990). The discrepancies may also be explained in a successional context. Later-successional species tend to produce seeds with limited longevity and dispersal abilities than early successional species (Major and Pyott 1966, Grime 1977, Thompson and Grime 1979, Moore 1980), although this relationship is not absolute (Leck et al. 1989). The successional model of the vegetation dynamics of the study area (Yeaton and Esler 1990) provided an opportunity to interpret the

seed-bank dynamics in terms of overall vegetation structure and turnover. An interesting observation is that those species which were proportionally over-represented in the seed bank (e.g. the more opportunistic species associated with *heuweltjies*, drainage lines and washes) were species identified as early successional by Yeaton and Esler (1990). All of these species have small seeds that do not germinate easily in laboratory trials (Chapter 3) and their seeds were found in all of the microhabitats that were sampled, whereas seeds of later successional species were mainly associated with adult plant cover. Most of the early successional species (adults) are associated with *heuweltjies* which were not sampled in this study. This suggests that these species have longer range dispersal and larger seed banks, an advantage when requirements are for opportunistic establishment. Later successional species had low levels of dormancy. Thompson and Grime (1979) and Thompson (1987) noted that species with larger seeds, often with awns or hairs and simple requirements for germination, often lacked seed banks. This is consistent with our findings for Pteronia pallens. Early successional species in this system appear to maintain larger seed banks than later successional species, although seed bank sizes are obviously far smaller than estimates for annual species.

5.5.1 Concluding remarks

The natural vegetation in the Karoo is used extensively for wool and mutton production (Roux 1968). Continuous, heavy grazing severely reduces seed production of all plant species found on the study site (Milton and Dean 1990). Since large seed banks are generally not maintained by species in this environment, heavy grazing coupled with low rainfall years may profoundly influence the dynamics of the vegetation. Seed banks, certainly of the more palatable, later successional species (e.g. P. pallens, O. sinuatum), are unlikely to persist beyond the life span of a perennial shrub. This makes preferred grazing species particularly vulnerable to local extinction as a result of heavy and continuous stocking of domestic livestock (O'Connor 1991).

5.6 REFERENCES

Adamson,R.S. 1955. Galenia L. South African species of Aizoaceae II. Journal of South African Botany 21:87-127.

Akaike,H. 1974. A new look at the statistical model identification. IEEE Transactions of Automatic Control AC-19:716-723.

Baker,R.J. and Nelder,J.A. 1978. The GLIM system. Numerical Algorithms Group, Oxford, England.

Beatley,J.C. 1980. Fluctuations and stability in climax shrub and woodland vegetation of the Mojave, Great Basin and transition deserts of southern Nevada. Israel Journal of Botany 28:149-168.

Brown,J.H., Reichman,O.J. and Davidson,D.W. 1979. Granivory in desert ecosystems. Annual Review of Ecology and Systematics 10:201-27.

Coffin,D.P. and Lauenroth,W.K. 1989. Spatial and temporal variation in the seed bank of a semi-arid grassland. American Journal of Botany 76:53-58.

Dean,W.R.J. and Yeaton,R.I. 1992. The importance of harvester ant Messor capensis nest-mounds as germination sites in the southern Karoo, South Africa. African Journal of Ecology 30:335-345.

Grime,J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist 111:1169-1194.

Gross,K.L. 1990. A comparison of methods for estimating seed numbers in the soil. Journal of Ecology 78:1079-1093.

Hassan,M.A. and West,N.E. 1986. Dynamics of soil seed pools in burned and unburned sagebrush semi-deserts. Ecology 67:269-272.

Henderson,C.B., Petersen,K.E. and Redak,R.A. 1988. Spatial and temporal patterns in the seed bank and vegetation of a desert grassland community. Journal of Ecology 76:717-728.

Hobbs,R.J. and Mooney,H.A. 1986. Community changes following shrub invasion of grassland. Oecologia 70:508-513.

Hoffman,M.T. 1989. A preliminary investigation of the phenology of subtropical thicket and karroid shrubland in the lower Sundays river valley, S.E. Cape. South African Journal of Botany 55:586-597.

Kemp,P.R. 1989. Seed banks and vegetation processes in deserts. In: Ecology of soil seed banks, eds. M.A. Leck, V.T. Parker and R.L. Simpson, Academic Press, New York. pp 257-281.

Leck,M.A. 1989. Wetland seed banks. In: Ecology of soil seed banks, eds. M.A. Leck, V.T. Parker and R.L. Simpson, Academic Press, New York. pp 283-205.

Leck,M.A., Parker,V.T., and Simpson,R.L. 1989. Ecology of soil seed banks, Academic Press, New York. 462pp.

Lovegrove,B.G. and Siegfried,W.R. 1986. The distribution and formation of mima-like mounds in the western Cape region of South Africa. South African Journal of Science 82:432-436.

Major,J. and Pyott,W.T. 1966. Buried, viable seeds in two California bunchgrass sites and their bearing of the definition of a flora. Vegetatio 13:253-282.

McAuliffe,J.R. 1988. Markovian dynamics of simple and complex desert plant communities. The American Naturalist 131:459-490.

McCullagh,P. and Nelder,J.A. 1983. Generalised Linear Models. Chapman and Hall, London. 261pp.

Milton,S.J. 1992. Effects of rainfall, competition and grazing on flowering of Osteospermum sinuatum (Asteraceae) in arid Karoo rangeland. Journal of the Grassland Society of South Africa 9:158-164.

Milton,S.J. and Dean,W.R.J. 1990. Seed production in rangelands of the southern Karoo. South African Journal of Science 86:231-233.

Milton,S.J., Dean,W.R.J. and Kerley,G.I.H. 1992. Tierberg Karoo Research Centre: history, physical environment, flora and fauna. Transactions of the Royal Society of South Africa 48:15-46.

Moore,P.D. 1980. Soil seed banks. Nature 284:123-124.

Nelson,J.F. and Chew,R.M. 1977. Factors affecting seed reserves in the soil of a Mojave desert ecosystem, Rock Valley, Nevada. American Midland Naturalist 97:300-321.

O'Connor,T.G. 1991. Local extinction in perennial grassland: a life-history approach. American Naturalist 137:753-773.

Parmenter,R.R. and MacMahon,J.A. 1983. Factors determining the abundance and distribution of rodents in a shrub-steppe ecosystem: the role of shrubs. Oecologia 59:145-156.

Price,M.V. and Reichman,O.J. 1987. Distribution of seeds in Sonoran desert soils: implications for Heteromyid rodent foraging. Ecology 68:1797-1811.

Pulliam,H.R. and Brand,M.R. 1975. The production and utilisation of seeds in plains grassland of southeastern Arizona. Ecology 56:1158-1166.

Reichman,O.J. 1984. Spatial and temporal variation of seed distributions in Sonoran desert soils. Journal of Biogeography 11:1-11.

Roberts,H.A. 1981. Seed banks in soils. Advances in Applied Ecology 6:1-55.

Roux,P.W. 1968. Veld management in the Karoo and adjacent sweet grassveld regions. In: Small stock industry in South Africa, ed. W.J. Hugo, Government Printer, Pretoria. pp 318-340.

Rutherford,M.C. and Westfall,R.H. 1986. The biomes of southern Africa - an objective categorisation. Memoirs of the Botanical survey of South Africa 54:1-98.

Smith,R.L. 1986. Elements of Ecology. Harper and Row, New York. 677pp.

Thompson,K. 1987. Seeds and seed banks. New Phytologist 106(supplement): 23-34.

Thompson,K. and Grime,J.P. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. Journal of Ecology 67:893-921.

Turner,R.M. 1982. Great Basin desert scrub. Desert Plants 4:145-155.

Van Rooyen,M.W. and Grobbelaar,N. 1982. Saadbevolkings in die grond van die Hester Malan-natuurreservaat in die Namakwalandse Gebrokeveld. South African Journal of Botany1:41-50.

Von Willert,D.J., Eller,B.M., Werger,M.J.A., Brinckmann,E., and

Ihlenfeldt,H.D. 1992. Life strategies of succulents in deserts: with special reference to the Namib desert. Cambridge University Press, Cambridge. 340pp.

Williams,D.A. 1982. Extra binomial variation in logistic linear models. Applied Statistics 31:144-148.

Yeaton,R.I. and Esler,K.J. 1990. The dynamics of a succulent karoo vegetation: a study of species association and recruitment. Vegetatio 88:103-113.

Zar,J.H. 1984. Biostatistical Analysis. Prentice-Hall, New Jersey. 718pp.

5.7 APPENDIX: DETAILS OF GENERALISED LINEAR MODELS

A) TOTAL NUMBER OF SEEDLINGS:
The model (Poisson distribution, log link) fitted to the total number of seedlings emerging from soil samples collected over two years (1 = 1989; 2 = 1990), two seasons (1 = summer/January; 2 = winter/July) and from three microhabitats (1 = open; 2 = under Ruschia spinosa; 3 = Brown-anthus ciliatus, referred to as site) was:

$$Log\ \mu_{ijk} = \mu + \alpha_i^{site} + \beta_j^{year} + \gamma_k^{season} + (\gamma_k \beta_j)^{season.year}$$

μ_{ijk} = true count made in the ith site, in the jth year and the kth season,
$\alpha_1 = \beta_1 = \gamma_1 = 0$.

A variance inflation factor, σ^2 of 11.99 was used to account for extra-Poisson variation. The variance in the observed count:
Var $(\mu_{ijk}) = \sigma_2.\mu_{ijk}$.

B) MEAN NUMBER OF SEEDLINGS PER SOIL SAMPLE:
The model (Poisson distribution, log link) fitted to the mean number of seedlings emerging from soil samples collected over two years (1 = 1989; 2 = 1990), two seasons (1 = summer/January; 2 = winter/July) and from three microhabitats (1 = open; 2 = under Ruschia spinosa; 3 = Brown-anthus ciliatus) was:

$$Log\ \mu_{ijk} = \mu + \alpha_i^{site} + \gamma_k^{season}$$

μ_{ik} = true count made in the ith site and the kth season,
$\alpha_1 = \gamma_1 = 0$.

Analysis of deviance table:

MODEL	RESIDUAL DEVIANCE	D.F.	DEVIANCE CHANGE	D.F.
mean	44.24	11		
mean + season	18.13	10	26.11	1
mean + season + site	3.03	8	15.10	2
mean + season + site + year	2.87	7	0.16	1

Chi squared goodness of fit for the model:

MODEL	χ^2	D.F.	AKAIKE'S ADJUSTMENT
mean	50.52	11	52.52
mean + season	18.70	10	22.70
mean + season + site*	3.21	8	11.21
mean + season + site + year	3.07	7	13.07

* = best fitting model by Akaike's criterion

The coefficients and standard errors for the final model:

VARIABLE	PARAMETER ESTIMATE	STANDARD ERROR
mean	1.356	0.3328
season 2	-1.606	0.3642
site 2	0.3312	0.4289
site 3	1.224	0.3722

The residuals showed no pattern and none were excessively large.

C) TIME TAKEN TO REACH 50% GERMINATION:
The model (Poisson distribution, log link) of the time taken for 50% of the total number of seedlings emerging from soil samples collected over two years (1 = 1989; 2 = 1990), two seasons (1 = summer/January; 2 = winter/July) and from three microhabitats (1 = open; 2 = under Ruschia spinosa; 3 = Brownanthus ciliatus) was:

$$Log\ \mu_{ijk} = \mu + \alpha_i^{site} + \beta_j^{year} + \gamma_k^{season} + (\gamma_k \beta_j)^{season.year}$$

μ_{ijk} = true count made in the ith site, in the jth year and the kth season,
$\alpha_1 = \beta_1 = \gamma_1 = 0$.

Analysis of deviance table:

MODEL	RESIDUAL DEVIANCE	D.F.	DEVIANCE CHANGE	D.F.
mean	112.66	11		
mean + season	27.95	10	84.71	1
mean + season + site	21.31	8	6.64	2
mean + season + site + year	12.88	7	8.44	1
main effects + season x site	10.75	5	2.13	2
main effects + season x year	11.66	6	1.22	1
main effects + year x site	4.46	5	8.42	2

Chi squared goodness of fit for the model:

MODEL	χ^2	D.F.	AKAIKE'S ADJUSTMENT
mean	-	-	-
mean + season	-	-	-
mean + season + site	19.57	8	25.57
mean + season + site + year	12.27	7	22.27
main effects + season x site	10.29	5	20.29
main effects + season x year	10.96	6	22.96
main effects + year x site*	3.81	5	17.81

* = best fitting model by Akaike's criterion

The coefficients and standard errors for the final model:

VARIABLE	PARAMETER ESTIMATE	STANDARD ERROR
mean	1.589	0.2592
season 2	-1.747	0.2256
site 2	0.031	0.2480
site 3	-0.079	0.2511
year 2	-0.047	0.2490
site 2 x year 2	-0.424	0.3784
site 3 x year 2	-1.292	0.4686

The residuals showed no pattern and none were excessively large.

D) SPECIES RICHNESS

The model (Poisson distribution, log link) fitted to the total number of seedling species emerging from soil samples collected over two years (1 = 1989; 2 = 1990), two seasons (1 = summer/January; 2 = winter/July) and from three microhabitats (1 = open; 2 = under Ruschia spinosa; 3 = Brownanthus ciliatus) was:

$$Log\ \mu_{ijk} = \mu + \alpha_i^{site} + \gamma_k^{season}$$

μ_{ik} = true count made in the ith site and the kth season,
$\alpha_1 = \gamma_1 = 0$.

Analysis of deviance table:

MODEL	RESIDUAL DEVIANCE	D.F.	DEVIANCE CHANGE	D.F.
mean	21.36	11		
mean + season	13.05	10	8.31	1
mean + season + site	5.28	8	7.77	2
mean + season + site + year	4.27	7	1.01	1

Chi squared goodness of fit for the model:

MODEL	χ^2	D.F.	AKAIKE'S ADJUSTMENT
mean	4.155	11	18.155
mean + season	12.530	10	16.530
mean + season + site*	5.042	8	13.042

* = best fitting model by Akaike's criterion

The coefficients and standard errors for the final model:

VARIABLE	PARAMETER ESTIMATE	STANDARD ERROR
mean	2.672	0.1556
season 2	-0.418	0.1467
site 2	0.334	0.1891
site 3	0.498	0.1830

The residuals showed no pattern and none were excessively large.

E) SEED DECAY OF FIELD-EXPOSED SEEDS

Generalised Linear models (binomial distribution, logit link) were fitted to the number of seeds remaining (out of 25) in seed bags (4 per treatment) placed on the soil surface (1) or buried at 2cm (2)(referred to as BURIAL) in three different microhabitats (referred to as SITE) and left in the field for up to two years. Microhabitats were 1 = open, 2 = under Ruschia spinosa and 3 = under Pteronia pallens. Seed bags were randomly retrieved from the field after 6, 12, 18 and 24 months of exposure (referred to as TIME).

1: Pteronia pallens:
Let π_{ijk} = the true proportion of seeds remaining, then we assume that:

$$Log \frac{\pi_{ijk}}{1 - \pi_{ijk}} = \mu + \beta^{time} + \alpha^{site} + \gamma^{burial}$$

$\beta_1 = \alpha_1 = \gamma_1 = 0.$

Analysis of deviance table:

MODEL	RESIDUAL DEVIANCE	D.F.	DEVIANCE CHANGE	D.F.
mean	518.72	95		
mean + time	229.87	92	288.90	3
mean + site	439.13	93	79.59	2
mean + burial	513.41	94	5.31	1
all main effects	132.79	89	385.90	6
all two way interactions	110.38	78	22.41	11
all three way interactions	92.58	78	17.80	

Phi for the full model = 0.0032
Phi for the model with the main effects only = 0.0288
new residual deviance for the model with all main effects = 72.89, d.f. = 89

2: Ruschia spinosa:
Let π_{ijk} = the true proportion of seeds remaining, then we assume that:

$$Log \frac{\pi_{ijk}}{1 - \pi_{ijk}} = \mu + \beta^{time} + \alpha^{site}$$

$\beta_1 = \alpha_1 = 0$.

Analysis of deviance table:

MODEL	RESIDUAL DEVIANCE	D.F.	DEVIANCE CHANGE	D.F.
mean	431.92	95		
mean + time	310.45	92	121.48	3
mean + site	356.59	93	75.33	2
mean + burial	431.88	94	0.04	1
all main effects	231.17	89	200.80	6
all three way interactions	146.71	72		

Phi for the full model = 0.0335
Phi for the model with the time and site effects only = 0.0892
new residual deviance for this model = 40.79, d.f. = 90

3: Brownanthus ciliatus:
Let π_{ijk} = the true proportion of seeds remaining, then we assume that:

$$Log \frac{\pi_{ijk}}{1 - \pi_{ijk}} = \mu + \beta^{time} + \alpha^{site} + \gamma^{burial}$$

$\beta_1 = \alpha_1 = \gamma_1 = 0$.

Analysis of deviance table:

MODEL	RESIDUAL DEVIANCE	D.F.	DEVIANCE CHANGE	D.F.
mean	640.10	95		
mean + time	478.01	92	162.10	3
mean + site	525.21	93	114.89	2
mean + burial	620.51	94	19.59	1
all main effects	333.18	89	306.90	6
all two way interactions	218.87	78	421.20	17
all three way interactions	186.24	72		

Phi for the full model = 0.0603
Phi for the model with the all main effects = 0.0603
new residual deviance for this model = 136.11, d.f. = 89

4: Galenia fruticosa:
Let π_{ijk} = the true proportion of seeds remaining, then we assume that:

$$Log \frac{\pi_{ijk}}{1 - \pi_{ijk}} = \mu + \beta^{time} + \alpha^{site} + \gamma^{burial}$$

$\beta_1 = \alpha_1 = \gamma_1 = 0$.

Analysis of deviance table:

MODEL	RESIDUAL DEVIANCE	D.F.	DEVIANCE CHANGE	D.F.
mean	299.90	95		
mean + time	229.39	92	70.51	3
mean + site	296.27	93	3.63	2
mean + burial	276.35	94	23.54	1
all main effects	201.36	89	98.54	6
all two way interactions	155.70	78	144.2	17
all three way interactions	138.34	72	161.6	23

Phi for the full model = 0.0327
Phi for the model with the all main effects = 0.0432
new residual deviance for this model = 114.95, d.f. = 91

5.8 APPENDIX: SPECIES RECORDED IN THE SOIL SEED BANK

List of species recorded in the soil seed bank from samples collected over two years (1989, 1990), two seasons (summer, winter) and three micro-habitats (open, and under Ruschia spinosa and Brownanthus ciliatus adult plants) at the Tierberg Karoo Research Centre, Cape Province, South Africa. Adult plant habitat and abundance data are from Milton et al. (1992), where P = plains, W = washes, D = drainage lines, H = *Heuweltjies*, A = abundant, C = common, O = occasional, R = rare and E = ephemeral.

Species	Habitat	Abundance
Aridaria noctiflora (L.)Schwant.	H,W,D	C
Augea capensis Thunb.	H,D	A
Brownanthus ciliatus (Ait.)Schwant.	H,W,D	C
Bulbine sp.	-	-
Crassula deltoidea Thunb.	P	O
Crassula muscosa L.	P,W	C
Crassula nudicaulus L. var platyphylla (Harv.)Toelk.	P,W	R
Crassula subaphylla (Eckl. & Zeyh.)Harv.	P,W	A
Drosanthemum cf. hispidum (L.)Schwant.	H,W,D	C
Drosanthemum lique (N.E.Br)Schwant.	W,D	C
Drosanthemum montaguense L.Bol.	P,W	A
Eriocephalus ericoides (L.f.)Druce	W,D	C
Euphorbia caterviflora N.E.Br.	P,W,H	C
Felicia filifolia (Vent.)Burtt Davy	W	C
Galenia fruticosa (L.f.)Sond.	P	A
Galenia papulosa Sond.	H	O
Gazania krebsiana Less.	P,W	C
Hereroa sp.	P	A
Hypertellus salsoloides (Burch.)Adamson	D	O
Leysera tenella D.C.	D	E
Lotononis cf. versicolor (E.Mey)Benth.	P,W,H	C
Malephora lutea Schwant.	H,W,D	A

Species	Habitat	Abundance
Mesembryanthemum cf. chrystallinum L.	H	C
Osteospermum sinuatum (D.C.)T.Norl.	P,H,W	A
Othonna protecta Dinter	P	O
Pentzia incana (Thunb.)Kuntz	W,D	C
Pentzia pilulifera (L.f.)Fourc.	H,D	A
Psilocaulon utile L.Bol.	H	A
Pteronia spp. (empetrifolia/pallens)	P,H,W	A
Rhinephyllum cf. graniforme (Haw.)L.Bol.	P	C
Rhinephyllum macradenium (L.Bol.)L.Bol.	P	A
Ruschia approximata (L.Bol.)Schwant.	P	C
Ruschia crassa	-	-
Ruschia spinosa Hartm. & Stuber (L.Bol)L.Bol.	P	A
Senecio angustifolius (Thunb.)Willd.	H,D	C
Sphalmanthus brevifolius (Haw.)N.E.Br.	P,H,W	C
Tetragonia echinata Ait.	H	C
Tetragonia spicata L.f. var spicate	P	C
Unidentified Mesembryanthema	?	?
Unidentified non-Mesembryanthema	?	?
Ursinia nana D.C.	P,D	O
Zygophyllum sp.	H,W	C

APPENDIX 5.9 Numbers of germinable seeds from soil collected over years (1989, 1990), two seasons (summer, winter) and three microhabitats (open and under Ruschia spinosa and Brownanthus ciliatus adults) from the Tierberg Karoo Research Centre, Cape Province, South Africa. Figures in parentheses are the proportions (%) of seeds with respect to the total number of seeds recorded in each microhabitat. Adult cover data % are from Yeaton and Esler (1990).

		SUMMER 1989			WINTER 1989			SUMMER 1990			WINTER 1990		
Species with adult cover > 1%	**Adult cover**	**Open**	**Under Ruschia**	**Under Brown-anthus**	**Open**	**Under Ruschia**	**Under Brown-anthus**	**Open**	**Under Ruschia**	**Under Brown-anthus**	**Open**	**Under Ruschia**	**Under Brown-anthus**
Pteronia spp.	32.3	0(0.0)	14(5.6)	23(3.8)	0(0.0)	0(0.0)	1(0.7)	0(0.0)	1(0.4)	3(0.4)	0(0.0)	4(10.0)	9(10.5)
Osteospermum sinuatum	4.9	0(0.0)	2(0.8)	1(0.2)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	1(0.4)	3(0.4)	0(0.0)	1(2.5)	1(1.2)
Galenia fruiticosa	12.1	33(27.3)	48(19.1)	54(8.9)	3(9.7)	16(15.8)	17(12.1)	143(50.4)	64(25.9)	183(24.9)	135(3.7)	3(7.5)	3(3.5)
Drosanthemum montaguense	4.2	0(0.0)	0(0.0)	3(0.5)	0(0.0)	0(0.0)	1(0.7)	0(0.0)	0(0.0)	2(0.3)	0(0.0)	0(0.0)	0(0.0)
Ruschia approximata	3.1	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	1(0.4)	1(0.2)	0(0.0)	0(0.0)	0(0.0)
Rhinephyllum macradenium	6.1	0(0.0)	3(1.2)	1(0.2)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	2(0.8)	6(0.9)	9(33.3)	1(2.5)	0(0.0)
Brownanthus ciliatus	6.6	6(5.0)	1(0.4)	343(56.6)	4(12.9)	9(8.9)	77(54.6)	25(8.8)	13(5.3)	395(53.7)	4(14.8)	1(2.5)	44(51.2)
Hereroa spp.	4.0	7(5.8)	5(2.0)	5(0.8)	1(3.2)	0(0.0)	1(0.7)	9(3.2)	3(1.2)	7(1.0)	2(7.4)	0(0.0)	0(0.0)
Ruschia spinosa	25.7	29(24.0)	76(30.2)	36(5.9)	3(9.7)	29(28.7)	8(5.7)	76(26.8)	61(24.7)	27(3.7)	6(22.2)	5(12.5)	6(7.0)
Species with adult cover < 1%													
Ruschia dolomitica	0.8	2(1.7)	6(2.4)	1(0.2)	0(0.0)	0(0.0)	0(0.0)	4(1.4)	8(3.3)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
Tetragonia spicata	0.2	1(0.8)	16(6.4)	25(4.1)	0(0.0)	5(5.0)	2(1.4)	0(0.0)	8(3.2)	27(3.7)	0(0.0)	0(0.0)	3(3.5)
Lotononis cf. versicolor	<1	1(0.8)	24(9.5)	8(1.3)	2(6.5)	2(11.9)	5(3.6)	7(2.5)	31(12.6)	20(2.7)	1(3.7)	19(47.5)	7(8.1)
Crassula spp.	<1	13(10.7)	20(8.0)	1(0.2)	4(12.9)	11(10.9)	5(3.6)	4(1.4)	27(10.9)	4(0.5)	0(0.0)	2(5.0)	1(1.2)
Flats Mesembryanthema	<1	12(9.9)	13(5.2)	29(4.8)	1(3.2)	5(5.0)	12(8.5)	13(4.6)	10(4.1)	16(2.2)	1(3.7)	1(2.5)	1(1.2)
Flats/washes spp.	<1	11(9.1)	22(8.7)	25(4.3)	11(35.5)	13(12.9)	14(9.9)	1(0.4)	5(2.0)	7(1.0)	0(0.0)	1(2.5)	0(0.0)
Heuweltjie Mesembryanthema	<1	4(3.3)	2(0.8)	50(8.3)	2(6.5)	1(1.0)	5(3.6)	2(0.7)	12(4.9)	28(3.8)	2(7.4)	0(0.0)	9(10.5)
Heuweltjie spp.	<1	2(1.7)	0(0.0)	1(0.2)	0(0.0)	0(0.0)	1(0.7)	0(0.0)	0(0.0)	6(0.8)	1(3.7)	2(5.0)	2(2.3)
Total number of seeds		121	252	606	31	101	149	284	247	735	27	40	86

CHAPTER 6

PATTERNS OF SEEDLING ESTABLISHMENT IN SEMI-ARID, SUCCULENT KAROO VEGETATION: THE ROLE OF FACILITATION AND DISPERSAL

6.1 ABSTRACT

Seedling establishment was monitored on the farm Tierberg in the Succulent Karoo of southern Africa. At approximately bi-monthly intervals over two years, ten strip transects were searched for newly germinated seedlings in seven microhabitats. Seedling survival was monitored in two successive years after two major recruitment events in April, when most rain fell in the study area. The timing and amount of rainfall and the frequency of follow-up rains influenced germination response as well as seedling survival. Less than 10% of the seedlings that germinated in 1989, and none of those that germinated in 1990, survived through the first post-germination year, highlighting the slow population turnover. Most of the seedlings recorded (78%) were from the monophyletic group, the Mesembryanthema. The location of seedlings varied widely among habitats. The majority of seedlings (61%) were found in the open, although litter sites (18%) and, to a lesser extent, sites under mat-forming Mesembryanthema (8%), were also favoured. The patterns of seedling distributions could be explained in terms of a model of the vegetation dynamics. However, the view that seedling recruitment of some species is facilitated by the presence of others was questioned, since seedling survival did not differ in different microhabitats. The dispersal characteristics of individual species may be more important in determining where seedlings are distributed; seedlings in supposedly more favourable microhabitats may not be nursed but rather trapped.

6.2 INTRODUCTION

In arid and semi-arid systems, low and variable rainfall has important effects on both the physiological and demographic characteristics of plants (Noy-Meir 1973, Westoby 1980). For example, the timing of flowering, seed-set, dispersal and germination is crucial where periods suitable for these processes are short and uncertain (Noy-Meir 1973). Seedlings are especially vulnerable to water stress and consequently germination and recruitment are the critical stages in the life cycles of many semi-arid plants. Although a certain threshold of rain may be required before a germination event can occur (Vidella and Armesto 1989), seedling survival depends on adequate post-germination rainfall (Steenbergh and Lowe 1969, Jordan and Nobel 1979, 1982, Castellanos and Molina 1990), and this is generally not predictable (Westoby 1980). By optimising timing of germination (Went 1949) and by recruiting into favourable microhabitats (Went 1942, Sherbrooke 1977, Soriano and Sala 1986), plants can avoid some of this resource unpredictability.

There have been very few studies on seed germination and seedling survival of karoo perennial plants. Henrici (1935, 1939) studied the germination and longevity of karoo shrub seeds, and more recently Dean and Milton (1991) and Dean and Yeaton (1992) investigated the importance of harvester ant nest mounds and mammal diggings as germination sites. Virtually nothing is known about optimum conditions for germination (Hoffman and Cowling 1987) and what effect habitat heterogeneity has on seed dispersal, germination and seedling establishment.

This chapter reports on the patterns of seedling germination and seedling survival in a plant community dominated by perennials in the semi-arid, southern Succulent Karoo. The study addressed the following questions:

1. *When do seedlings establish in the field? Is there any evidence for discrete periods of seedling establishment?*
2. *Is seedling establishment microhabitat specific? In which microhabitats do most seedlings occur and why?*

Yeaton and Esler (1990) observed that certain early successional species act as nurse plants for seedlings of a later successional woody guild. This conclusion was based on patterns observed in established seedlings. The present study provides a more detailed investigation into the early seedling emergence stage. The aim was to determine whether the patterns observed by Yeaton and Esler (1990) actually occurred at the emergence stage and if, in fact, seedling recruitment of some species is facilitated by the presence of others (i.e. "nursed").

The Karoo covers approximately 33% of South Africa's land surface (Rutherford and Westfall 1986) and is utilised extensively for wool and mutton production (Roux 1968). An understanding of the temporal and spatial patterns of seedling establishment is important for managers since these influence population turnover and therefore maintenance of cover (Grubb 1977, Harper 1977). Most of the species on the study site reproduce by sexual reproduction (seed) as opposed to vegetative reproduction (Milton and Dean 1990), thus seedling biology is of key importance in understanding plant population dynamics.

6.3 STUDY SITE

The study was conducted at the Tierberg Karoo Research Centre (Milton et al. 1992) near Prince Albert in the Succulent Karoo (33°10'S, 22°17'E). The area is situated on a colluvial plain (800 m altitude), 20 km north of the Swartberg mountain range of the Cape Folded Belt. The area receives approximately 170 mm of rain per year (Milton et al. 1992), falling mainly in autumn (March-May) and spring (September-November). Climate patterns at Tierberg are complex, but significant rainfall events (those greater than 10 mm, Sala and Lauenroth 1982) are more predictable in autumn (Chapter 1). Temperatures range from -5°C in winter to 43°C in summer, with a mean annual temperature of 17.5°C (Milton et al. 1992). The soils on the site are weakly structured sandy loams (Ellis and Lambrechts 1986).

The vegetation of the area has a high proportion of perennial succulent shrubs (mostly belonging to the monophyletic group, the Mesembryanthema in the family Aizoaceae) and non-succulent shrubs (family Asteraceae) and a very low cover of grasses (< 1%) (Milton et al. 1992). *Heuweltjies* or mima-like mounds (Lovegrove and Siegfried 1986), which support a set of species distinct from the surrounding vegetation, are evenly distributed over the study site at a mean density of 2.33 ± 0.11 per ha^{-1} (Milton et al. 1992).

6.4 METHODS

6.4.1 Field germination

At approximately bi-monthly intervals over a two year period (from January 1989 to January 1991), ten 100 m x 1 m strip transects in a 50 ha area within the study site were carefully searched for newly germinated seedlings. Prior to the first large germination event in April 1990, the entire transect area was surveyed (1000 m^2). However, this method was not practical for sampling small seedlings (<5 mm) when their numbers were high. The sampling technique was therefore adjusted, and from 29 April 1990, ten circular quadrats (290 mm in diameter) were placed every ten meters along each transect. Seedlings too abundant to quantify in the large transects were recorded within these quadrats (total quadrat area monitored: 26.43 m^2). Seedlings of Augea capensis Thunb. (Zygophyllaceae); Lotononis cf. versicolor (E.Mey) Benth. (Fabaceae); Osteospermum sinuatum (DC.) T. Noel. (Asteraceae); Pteronia spp. (Asteraceae) and Tetragonia spicata L.f var spicata (Tetragonioideae, Aizoaceae) were easily identified and occurred in sufficiently low numbers to be monitored over the entire strip transect area throughout the sampling period. Seedlings of Galenia fruticosa (L.f.) Sond. (Aizooideae, Aizoaceae) were too abundant to be accurately counted over the entire transect area so were recorded within the quadrats. Seedlings of the Mesembryanthema group (sub-families Mesembryanthemoideae and Ruschioideae in the family Aizoaceae), and other unidentified seedlings were too small and too abundant to

be easily counted and were therefore recorded within the quadrats. It was not possible to identify seedlings of Mesembryanthema spp. and Pteronia spp. To adjust for the different sampling techniques, seedling numbers were expressed per m^2.

Seedlings were recorded in seven microhabitats (similar to those in Yeaton and Esler 1990). These were:
1. In open areas on fine sands or clays between adult plants (open); 2. At the side of soil-mounds accumulated around adult plants (mound-side); 3. Under the canopy of adult Mesembryanthema with erect, shrub-like growth forms (woody branches and long internodes) (mesemb-shrub); 4. Under the canopy of adult Mesembryanthema spp. with mat-forming growth forms (mesemb-mat); 5. Under dead Mesembryanthema spp. (dead mesemb); 6. Under the canopies of other woody shrubs (not Mesembryanthema spp.) (shrub); and 7. In litter accumulated on the soil surface (litter). Litter is defined here as small pieces of plant material (excluding large branches), which lie loose on the soil surface (Facelli and Pickett 1991). Each of the microhabitats is referred to in this chapter according to the names given in parentheses.

The frequency of microhabitats over the ten 100 m x 1 m transects was determined using wheel point sampling (Tidmarsh and Havenga 1955). A preliminary survey was conducted to determine the accuracy of this method where "actual" microhabitat frequencies (measurements along a 100 m line transect) were compared with results obtained from the wheel point method. A comparison of results yielded no significant differences, thus the wheel point method was chosen.

6.4.2 Seedling survival

Field seedling survival was monitored after the recruitment events in April 1989 and April 1990. At the beginning of the monitoring periods to assess survival, it was assumed that most seedlings had germinated, and that no mortality had occurred. In April 1989, seedlings of Galenia fruticosa (n = 60), Pteronia spp.

(n = 43) and Osteospermum sinuatum (n = 8) were individually tagged. Seedling survival was monitored until March 1990. Sample sizes were small due to low seedling densities after this recruitment event. In April 1990, seedling survival was monitored from within the quadrats (described under Field germination, 6.4.1, above). Owing to the abundance of seedlings, sample sizes were large (n = 2 499, 357 and 57 respectively). In addition to the three species monitored in 1989, seedling survival of Mesembryanthema spp. was also monitored (n = 1 578). Sample sizes in 1990 were large enough to quantify variations in survival across microhabitats (described under Field germination, 6.4.1, above).

6.4.3 Environmental Data

Rainfall and temperature data were obtained from an automatic weather station established on the Tierberg study site (W.R.J. Dean, personal communication, Fitzpatrick Institute, University of Cape Town). In addition, a data logger was used to record soil temperature and soil moisture (1 cm below the soil surface) in three microhabitats during 1990. These were the open, mesemb-mat and shrub microhabitats described in the field germination section. Only three of the seven microhabitats were monitored because of limitations to the number of probes that could be linked up to the data logger.

6.4.4 Statistical analysis

Chi-squared tests on observed versus expected seedling emergence data were conducted to determine if the numbers of seedlings observed in different microhabitats in the field corresponded with microhabitat frequencies. Kendall's rank tests were used to test if the numbers of surviving seedlings were a function of the initial numbers of seedlings germinating in each microhabitat. The statistical computer programme, Statgraphics 5.0 (STSC Inc.), was used in both cases.

6.5 RESULTS

6.5.1 Field Germination

Two major germination events were recorded during the two year monitoring period. Both events occurred in April, following large rainfall events (> 50 mm), and when the ambient temperatures were declining after the hot summer months (Fig. 6-1). The coldest winter temperatures were recorded approximately three months after the germination events (in July) (Fig. 6-1). Rainfall totals in 1989 and 1990 were 245.5 mm and 193 mm respectively. The heaviest rains occurred between February and April in both years (Fig. 6-1), although more rain fell in this period in 1990. Rainfall one month prior to the 1989 germination event was 38.5 mm. In 1990, this amount was 50.3 mm. Less than 10 seedlings per m^2 were recorded in 1989. In 1990, more than 75 seedlings per m^2 were recorded immediately after the recruitment event (Fig. 6-1).

Most of the seedlings recorded (98%, after a recruitment event in April 1990) were of perennial shrubs. The majority of seedlings recorded (78%) were from the monophyletic group the Mesembryanthema. Next most abundant were Galenia fruticosa seedlings (14%) followed by those of Pteronia spp. (3%) (Table 6-1, Fig. 6-2). Forty seven to 51% of the adult plant cover (which make up more than 1% of the relative cover on the site) belongs to the Mesembryanthema. Galenia fruticosa comprises 12 to 25% and Pteronia spp., 13 to 32% of the vegetation cover (Yeaton and Esler 1990) (Fig. 6-2). All of the species recorded, except for Osteospermum sinuatum and Tetragonia spicata, were more abundant in the 1990 germination event (Fig. 6-2).

Seedling distributions were distinctly patchy (Tables 6-1, 6-2). Variance to mean ratios indicated that seedling distributions at the microhabitat scale were more heterogeneous than the distribution of adult plants on the study site (Table 6-2). At a broader, "transect" scale, (i.e. between transects), patchiness of Mesembryanthema spp., Tetragonia spicata and Pteronia spp. seedlings was still greater

than that of adult plants at the same scale. This was not the case for Galenia fruticosa or Osteospermum sinuatum seedlings. Temporal heterogeneity of seedlings was high, although not necessarily greater than spatial heterogeneity at a microhabitat scale (Table 6-2). The abundance of Osteospermum sinuatum seedlings varied the least in time, whereas Galenia fruticosa and Pteronia spp. seedlings were strongly variable in time.

The location of seedling species varied widely among microhabitats. The majority of seedlings (61%) were found in open microhabitats, although litter (18%) and to a lesser extent mesemb-mat microhabitats (8%) were also favoured (Table 6-1). Mesembryanthema spp., Galenia fruticosa and Lotononis sp. were mostly found in open microhabitats (Table 6-1). All of these species have small seeds which are either passively dispersed, or dispersed by water. Osteospermum sinuatum, Pteronia spp., Tetragonia spicata and Augea capensis seedlings were mostly found in litter and to a lesser extent in mesemb-mat sites. Seedlings of these species all have large, winged or plumed seeds which are dispersed by wind.

More Galenia fruticosa seedlings (immediately after the 1990 germination event) were found in open, mound-side, mesemb-shrub and litter sites than expected, given the actual frequency of microhabitats in the field (Table 6-3). The numbers of Pteronia spp. germinating in mesemb-mat and litter sites were greater than expected (Table 6-3). The observed numbers of Mesembryanthema spp. seedlings were approximately the same as expected in open microhabitats, and greater than expected in litter sites.

6.5.2 Seedling Survival

Less than 10% of the seedlings that germinated in 1989, and none of those that germinated in 1990, survived through the first post-germination year. Seedlings survived for longer in 1989 than in 1990 (Table 6-4). Rain was evenly spread throughout the year in 1989, with substantial rains falling in the summer months between October and December (Fig. 6-1). There was little post-germination

rainfall in 1990, and no rain fell in the summer months.

The differences in seedling survival rates were used to measure the "suitability" of each microhabitat. There were no marked differences in the rates of seedling mortality (as measured by the time taken to reach 50% mortality) between microhabitats (Table 6-5). The microhabitats where the majority of seedlings were recorded, were not necessarily the most favourable with respect to the rates of seedling survival (Table 6-5) - although the differences were only marginal. For example, Mesembryanthema seedlings survived the longest in mesemb-shrub and mound-side microhabitats, despite the fact that the majority of seedlings were recorded in open microhabitats. Despite these subtle differences in rates of seedling survival, the actual numbers of surviving seedlings appeared to be a function of the initial numbers of seedlings germinating in each microhabitat (Table 6-3). A significant relationship between the number of germinated and survived seedlings in different microhabitats was found for Pteronia spp. (Kendall's rank test, $P \leq 0.0457$, $r = 0.651$). The Kendall rank tests for Galenia fruticosa ($P \leq 0.156$, $r = 0.4763$) and Mesembryanthema ($P \leq 0.1832$, $r = 0.4606$) were non-significant, despite similar trends, possibly due to the large number of zero values in the data.

There were a few consistent temperature differences between the microhabitats monitored (Fig. 6-3). The highest monthly average and mean maximum temperatures were recorded in open microhabitats. The lowest monthly average temperatures were recorded under Pteronia pallens. The lowest mean minimum temperatures were recorded under Pteronia pallens and the highest mean minimum temperatures under Ruschia spinosa. Open microhabitats tended to be more extreme with respect to maximum temperatures, but not in terms of minimum temperatures. Although covered microhabitats were only marginally different with respect to average and maximum monthly temperatures, minimum temperatures under P. pallens were always low (Fig. 6-3). Coefficients of variation of daily temperature data indicated that the Pteronia pallens microhabitats were more variable throughout the year with respect to temperature fluctuations, especially

in terms of daily minima. Open sites, and sites associated with Ruschia spinosa had less variable temperature regimes (Table 6-6). There were no consistent patterns in the soil-moisture of the microhabitats monitored (Fig. 6-4). Soil-moisture readings were highest in one of the open sites and in one of the nurse sites. An increase in soil moisture was recorded from April to August of 1990, corresponding with the rainfall during this period (Fig. 6-1b).

Table 6-1. The numbers of seedlings per m^2 in seven microhabitats at the Tierberg Karoo Research Centre in the southern Karoo. Seedling abundances were monitored after a germination event in April 1990.

SPECIES	MICROHABITAT						
	Open	Mound -side	Litter	Mesemb-shrub	Mesemb-mat	Dead mesemb	Shrub
Mesembryanthema	40.560	1.513	8.210	2.837	4.465	0.038	2.081
Galenia fruticosa	4.654	2.005	2.573	0.870	0.416	0.038	0.492
Osteospermum sinuatum	0.003	0	0.012	0	0.009	0.001	0
Tetragonia spicata	0.002	0.002	0.050	0.008	0.060	0.001	0.006
Pteronia spp.	0.004	0.025	1.729	0.001	0.568	0.045	0.115
Lotononis sp.	0.681	0.303	0.341	0	0.114	0.076	0.114
Augea capensis	0	0	0.114	0	0	0	0
Other spp.	0.567	0.038	0.529	0.076	0.265	0	0.227
Total	46.47	3.89	13.56	3.79	5.90	0.20	3.03

Table 6-2. Spatial and temporal heterogeneity of adult plants and seedlings (as measured by variance to mean ratios) at the Tierberg Karoo Research Centre in the southern Karoo. Seedlings were counted immediately after a recruitment event on 29 April 1990.

SPECIES	SPATIAL HETEROGENEITY			TEMPORAL HETEROGENEITY
	ADULTS[1]	SEEDLINGS		SEEDLINGS[3] TRANSECT
		TRANSECT[1]	MICROHABITAT[2]	
All species	14.76	0.89	969.25	-
Mesembryanthema	10.74	26.03	665.95	634.06
Galenia fruticosa	20.12	4.58	49.28	1047.30
Tetragonia spicata	2.72	10.92	39.34	31.38
Osteospermum sinuatum	4.30	2.42	5.89	8.75
Pteronia spp.	4.36	212.37	1188.24	824.90

[1] = variance to mean ratios of adult plants and seedlings in ten, 100 x 1 m strip transects at one recording period (29 April 1990).

[2] = variance to mean ratios of seedlings among seven distinct microhabitats at one recording period (29 April 1990).

[3] = variance to mean ratios of total numbers of seedlings counted over five sampling periods from 29 April 1990 to 29 January 1991. All of the seedlings were from the same original cohort which germinated immediately prior to the first recording period. These ratios reflect the relative survivorship of each seedling species.

Table 6-3. Comparison between observed (OBS.) and expected (EXP.) seedling numbers at the Tierberg Karoo Research Centre, in the southern Karoo. Seedlings were counted immediately after a recruitment event on 29 April 1990 (germinated) and nine months later on 29 January 1991 (survived); and expected seedling numbers were calculated from the relative frequency of identified microhabitats (see section 6.4.1). Chi-squared tests were used to test for differences between observed and expected numbers of germinated seedlings.

MICROHABITAT	FREQUENCY OF MICROSITE	GERMINATED		X^2	SURVIVED	
		OBS.	EXP.		OBS.	EXP.
1) Galenia fruticosa						
Open	0.650	292	189.8	55.03	32	23.4
Mound-side	0.142	53	12.3	134.67	1	5.1
Mesemb-shrub	0.028	23	8.2	26.71	0	1.0
Mesemb-mat	0.062	11	18.1	2.79	2	2.2
Dead mesemb	0.009	1	2.6	-	0	0.3
Shrub	0.055	13	16.1	0.60	0	2.0
Litter	0.053	68	15.5	177.82	1	1.91
		X^2 = 397.6				
		d.f. = 5				
		Sig. = ***				
2) Pteronia spp.						
Open	0.650	7	1624.4	1610.4	2	34.5
Mound-side	0.142	25	354.9	306.6	2	7.5
Mesemb-shrub	0.028	10	70.0	51.4	0	1.5
Mesemb-mat	0.062	568	154.9	1101.9	14	3.3
Dead mesemb	0.009	45	22.5	22.5	0	0.5
Shrub	0.055	115	137.5	3.7	3	2.9
Litter	0.053	1729	132.4	19246.5	32	2.8
		X^2 = 22349.7				
		d.f. = 5				
		Sig. = ***				
3) Mesembryanthema spp.						
Open	0.650	1087	1035.5	2.6	14	13.0
Mound-side	0.142	40	226.2	153.3	0	2.8
Mesemb-shrub	0.028	75	44.6	20.7	6	0.6
Mesemb-mat	0.062	118	98.8	3.7	0	1.2
Dead mesemb	0.009	1	14.3	-	0	0.2
Shrub	0.055	55	87.6	12.1	0	1.1
Litter	0.053	217	84.4	208.2	0	1.1
		X^2 = 400.7				
		d.f. = 5				
		Sig. = ***				

Table 6-4. Time (days) taken for seedlings of four species at the Tierberg Karoo Research Centre in the southern Karoo to reach 50% mortality. Seedlings (sample sizes shown in parentheses) were monitored after recruitment events in April 1989 and 1990.

SPECIES	DAYS TO 50% MORTALITY	
	1989	1990
Pteronia spp.	162 (43)	66 (2499)
Galenia fruticosa	197 (60)	74 (357)
Osteospermum sinuatum	206 (8)	61 (57)
Mesembryanthema spp.	-	53 (1578)

Table 6-5. Time (days) taken for seedlings of four species in seven microhabitats at the Tierberg Karoo Research Centre in the southern Karoo to reach 50% mortality. Seedlings (sample sizes shown in parentheses) were monitored after a recruitment event in April 1990.

MICROHABITAT	DAYS TO 50% SEEDLING MORTALITY			
	Mesembryanthema	Pteronia spp.	Osteospermum sinuatum	Galenia fruticosa
Open	73 (1087)	51 (7)	- -	76 (292)
Mesemb shrub	85 (75)	- -	- -	- -
Mound side	83 (40)	69 (25)	- -	73 (53)
Mesemb mat	80 (118)	67 (568)	56 (36)	74 (11)
Litter	75 (217)	65 (1729)	71 (12)	73 (68)
Shrub	74 (55)	69 (115)	55 (5)	71 (13)
Dead mesemb	- -	58 (45)	- -	- -

Table **6-6.** Coefficients of variation of average, maximum and minimum temperatures recorded daily in three microhabitats.

	MICROHABITAT		
	open	shrub	mesemb-mat
Minimum	43.9	385.7	37.8
Maximum	13.1	15.0	13.7
Average	15.9	17.2	15.9

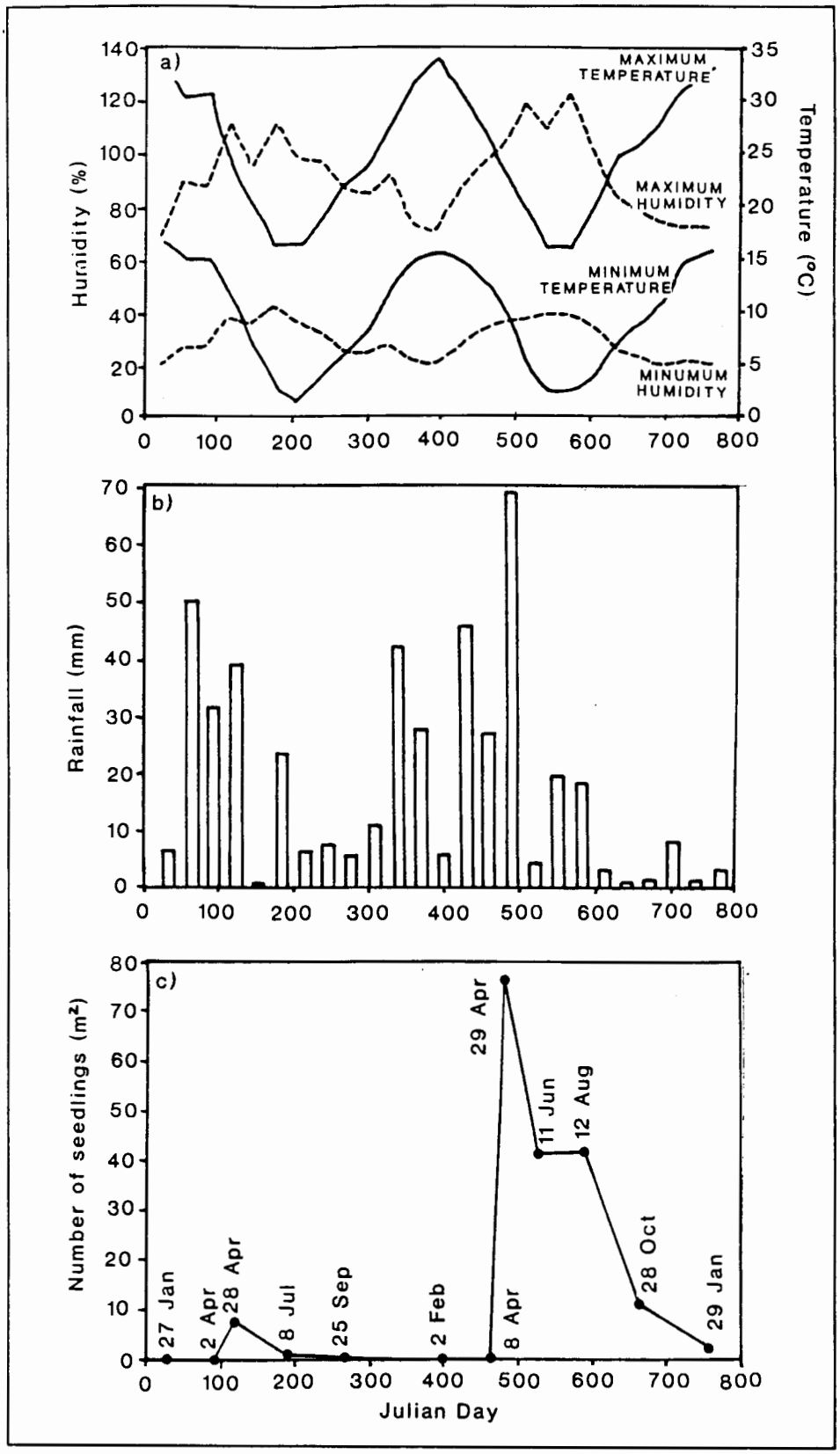

Figure 6-1. a) temperature and humidity, b) rainfall and c) number of seedlings per m^2 recorded over a two year period at the Tierberg Karoo Research Centre in the southern Succulent Karoo.

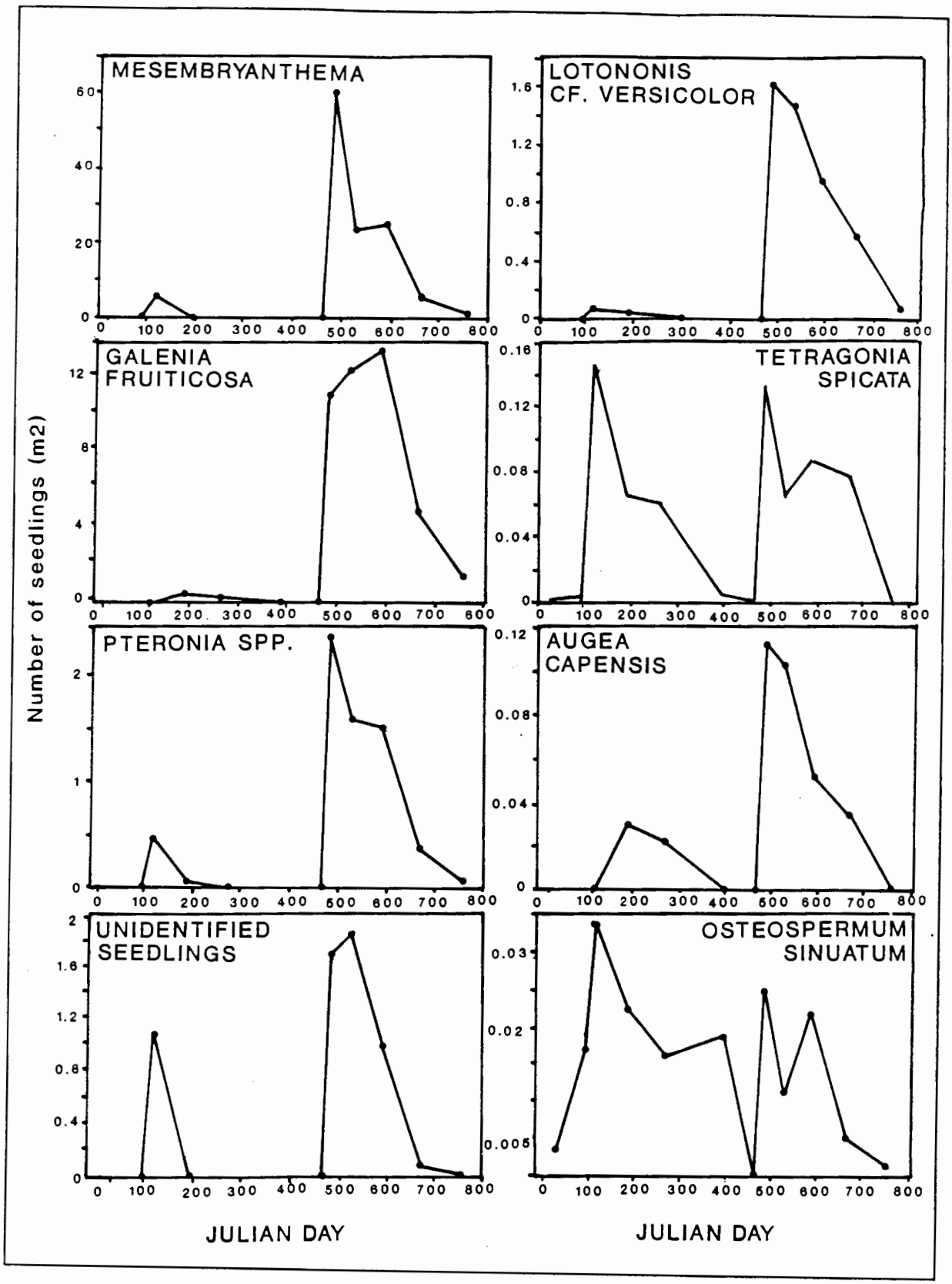

Figure 6-2. Number of seedlings per m^2 of selected species recorded over a two year period at the Tierberg Karoo Research Centre in the southern Succulent Karoo.

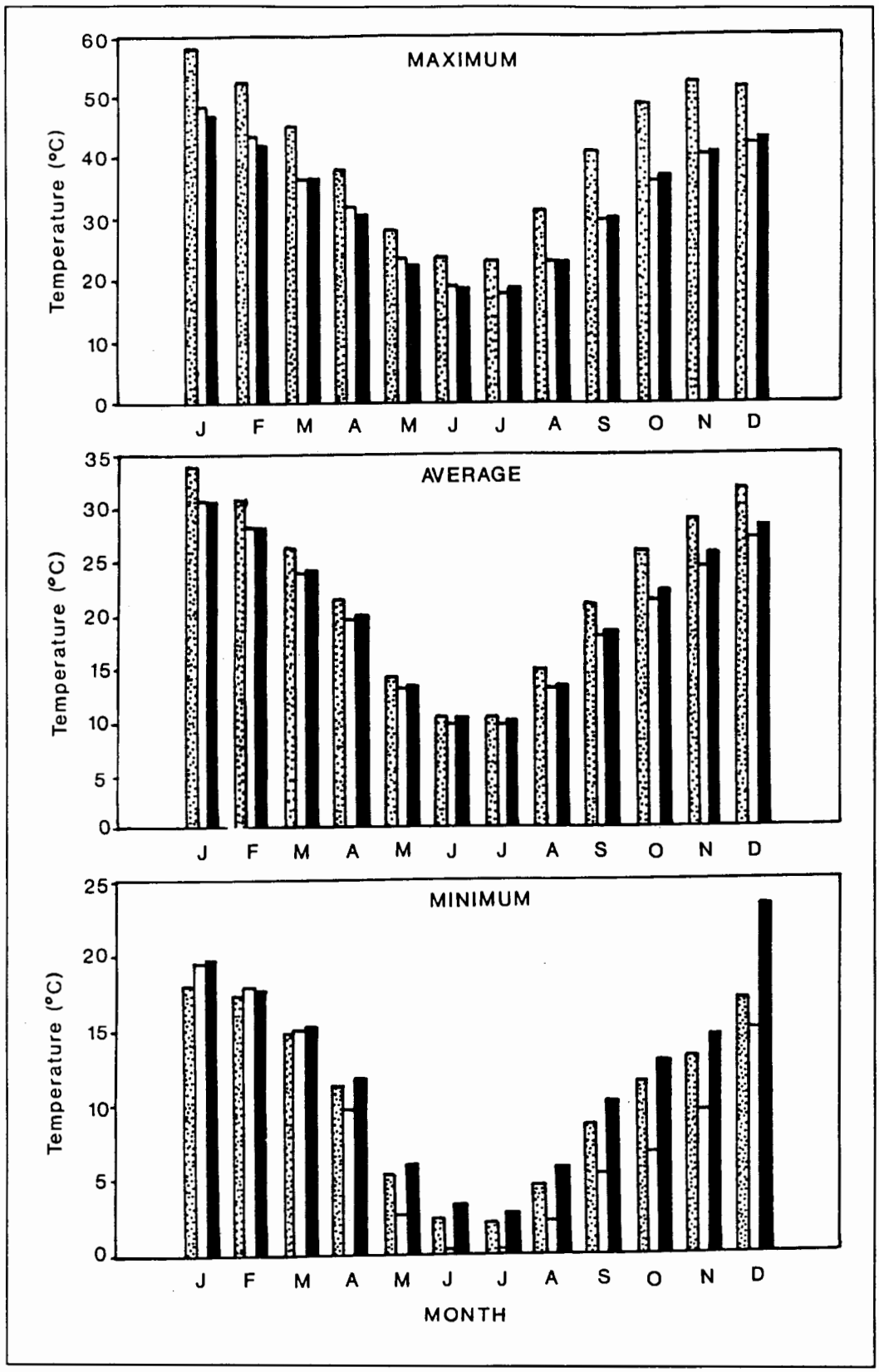

Figure 6-3. Mean maximum, average and minimum soil temperatures recorded in three microhabitats (open; under tall woody shrubs and under mesemb-mats) at the Tierberg Karoo Research Centre in the southern Succulent Karoo.

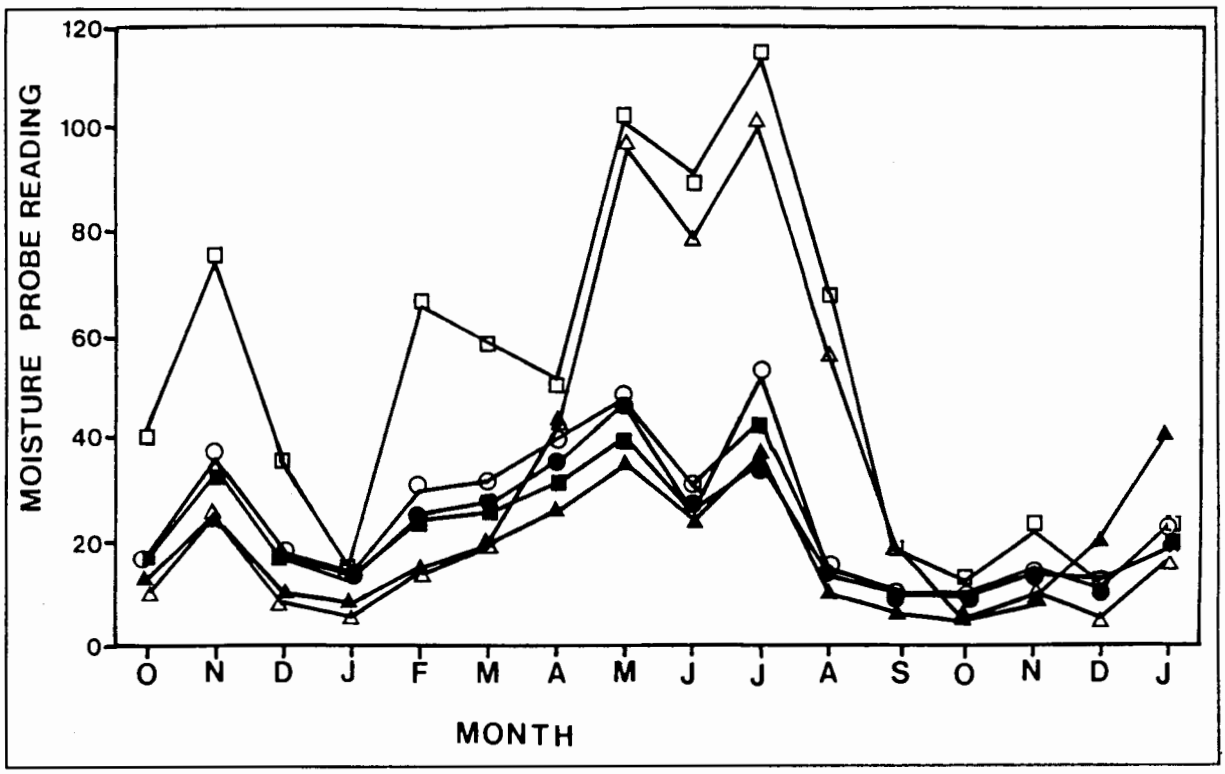

Figure 6-4. Soil moisture recorded in three microhabitats (open; under tall woody shrubs and under mesemb-mats) at the Tierberg Karoo Research Centre in the southern Succulent Karoo. (△,▲) = open, (■,●) = under woody shrubs, (□,○) = under mesemb-mats. Calibrations were not performed. However, soil water content is proportional to the electrical moisture probe reading.

6.6 DISCUSSION

When do seedlings germinate in the field? Is there any evidence for discrete periods of recruitment?

This study has shown that successful establishment of perennial species in the southern Karoo is influenced by the timing of rainfall events, the amount of rainfall prior to germination and the amount of rainfall following germination.

Two discrete germination events were recorded during this study. Both events occurred in April when ambient and soil temperatures were declining after the hot summer months. Climate patterns at Tierberg are complex, but rainfall events are more predictable in April when seedling germination was recorded. There is also a greater probability of follow-up rains during this period (Chapter 1). This confirms observations by Dean and Yeaton (1992) who studied harvester ant nest mounds as germination sites in the same study area. Although rain falls during the summer months at Tierberg (Milton et al. 1992), high temperatures probably prevent seedling germination and seedling survival (Dean and Yeaton 1992). No germination was recorded during the summer of 1989, despite several significant rain events (rainfall events greater than 10 mm are regarded as being significant in semi-arid areas, Sala and Lauenroth 1982). Noble and Crisp (1980) argue that germination in semi-arid Australian rangelands is closely related to the length of time that soil surface layers remain moist, and that this length of time is a function of temperature and rainfall. It must also be noted that seed banks on the study site are generally small and seasonal (i.e. transient) (Chapters 4 and 5). This means that recruitment events are likely to be tied up with the phenology of the species on the study site. Flowering on the study site occurs mostly during spring and seed dispersal during late summer/autumn (Hoffman 1989, Milton 1992). The April rains thus coincide with the period of greatest seed abundance on the study site. An understanding of flowering and dispersal periods is critical to understanding recruitment; this is an area which requires more research. Another factor which may have influenced the timing of germination is related to

germination control. Species occurring on the flats show significantly higher overall germination under a temperature regime which simulates the cooler autumn/spring conditions (Chapter 3, Henrici 1935).

The number of seedlings that germinated in each event appeared to be related to the amount of rainfall prior to recruitment. More seedlings were recorded after the larger rainfall events in April 1990, than those in April 1989. Although the degree of germination response may be related to the abundance of seeds in a particular year, a study of the size of the seed banks in 1989 and 1990 at Tierberg (Chapter 5) did not detect a significant year effect. Thus it is unlikely that differences in the 1989 and 1990 recruitment events were a result of seed source differences. The results should, however, be interpreted with a degree of caution, since they were based on only two years of data. Confounding factors such as herbivore pressure on seedlings and competition can not be discounted (Fonteyn and Mahal 1981, Parker 1982, McAuliffe 1986, Owens and Norton 1989).

Seedling survival of long-lived perennials in arid environments is generally low (Turner et al. 1966, Steenbergh and Lowe 1969, Turner et al. 1969, Crisp 1978, Castellanos and Molina 1990) and this study proved no exception. Very few seedlings survived past the first post-germination year. This indicates the slow vegetation dynamics in this semi-arid environment and suggests that follow-up rains are also of critical importance to seedling survival. Rain fell at regular intervals throughout 1989 whilst in 1990, there was very little post-germination rainfall. Although fewer seedlings germinated in 1989, these survived for longer periods than seedlings which germinated in the 1990 event.

The study was based in a community dominated by perennial shrubs. A very high proportion of seeds of perennial species is lost between the seed production stage and the seedling establishment phase. These losses may or may not have a corresponding impact on recruitment (Harper 1977) but the significance of these losses to population dynamics is difficult to determine. This is especially so in semi-arid environments where successful recruitment events (i.e. when seedlings

survive to maturity) are difficult to detect. This is because seedling establishment is either episodic and, therefore, temporally variable (e.g. after unusually favourable rainfall) or small but continuous, and therefore, spatially variable (e.g. if the probability of finding a favourable microhabitat is very low). Long-term data are needed to understand the influences of extreme climatic conditions on germination and recruitment. Only long-term monitoring and manipulative experiments (e.g. seed additions, Crawley 1990) will detect whether seedling losses have a significant effect on population dynamics.

Is germination/recruitment microhabitat specific? What microhabitats are important?

Seedlings were not uniformly distributed with respect to microhabitat and it appears that these patterns were largely a result of the dispersal biology of individual species. Seedling distributions were strongly patchy and variation in seedling abundances between microhabitats was considerable. Seedlings originating from wind-blown seeds were commonly associated with adult plant cover (mesemb-mat sites) and litter. For example, 70% of the Pteronia spp. seedlings were recorded in litter, and 23% in mesemb-mat sites. Species with passively dispersed seeds, or seeds dispersed by water, were more commonly found in open microhabitats. For example, 68% of the Mesembryanthema seedlings were found in the open. An alternative explanation for the seedling distribution patterns is that germination conditions in these microhabitats were the most suitable for each species, the assumption being that the patterns would not exist prior to germination. However, a study of the soil seed-banks indicated that corresponding seed distribution patterns did exist prior to germination (Chapter 5).

Mortality did not vary with respect to microhabitat. The numbers of seedlings establishing in different microhabitats appeared to be a function of the initial number of seedlings germinating and not a function of differential survival in each microhabitat. In other words, the microhabitats where the most seeds germinated were also those where the most seedlings survived. This challenges the view in

the dynamics model (Yeaton and Esler 1990) that seedling recruitment of some species is facilitated by the presence of others. It appears that the dispersal characteristics of individual species are more important: seedlings found in supposedly more favourable microhabitats may not be "nursed" but, rather, "trapped".

The nurse-plant phenomenon has been described for a variety of semi-arid environments (McAuliffe 1988), including the southern Succulent Karoo (Beukman 1991). Beukman (1991) and Dean and Yeaton (1992) suggested that the occurrence of seedlings under "nurses" was primarily a method of avoiding abiotic stress at the seedling stage. Unfortunately, descriptive accounts cannot reveal the dependence of seedlings on nurses. Differences in the relative tolerances of seedlings to water stress have, however been demonstrated (Chapter 7). Pteronia pallens and Osteospermum sinuatum seedlings (woody shrubs with wind blown seeds) are less tolerant to water stress than are Ruschia spinosa seedlings (Mesembryanthema with water dispersed seeds)(Chapter 7). This places some degree of uncertainty on the statement that seedlings may not be "nursed" but, rather, "trapped". Perhaps the dispersal characteristics of the species ensure that seedlings germinate into microhabitats with "suitable" site characteristics, best suited to their physiological requirements.

The nurse-plant phenomenon is assumed in the model of the dynamics of the vegetation on the study site. In the model, mound-building species of Mesembryanthema (mesemb-mats) are colonisers of open areas between existing vegetation. Mesemb-mats then provide woody shrubs with supposedly protected sites in which to establish. In time, the mat-forming Mesembryanthema are out-competed and replaced by the woody shrub guild (Yeaton and Esler 1990). Although the model was based on observations of established seedlings, the data confirms that these patterns occur at the seedling emergence stage. In this study, most of the Mesembryanthema seedlings germinated in open microhabitats. Species belonging to the woody shrub guild (Osteospermum sinuatum, Tetragonia spicata, Pteronia spp.) were more abundant in mesemb-mat microhabitats than in

open, shrub or mesemb-shrub microhabitats. A divergence from the model was that many seedlings germinated in litter microhabitats. Litter has a variety of well documented effects on seed capture, germination and recruitment (Fowler 1986, 1988). The data shows that litter plays a role in the spatial organisation of seedlings (at least of some species). Important questions like, "How does plant litter affect species diversity and plant abundance?" and, "How do different management strategies affect litter production?" require further research.

There are several implications to microhabitat specific germination. Firstly, it is possible that the availability of "suitable" microhabitats in the community regulates the relative abundances of recruiting individuals of certain species. This has important implications both for management and restoration ecology. If recruitment is microhabitat limited, then it is possible that herbivory (resulting in the removal of a large proportion of the seed source) would not have as great an impact on recruitment as pastoralists are led to believe (Milton 1992). Again, one needs to establish whether recruitment is seed-limited or not (Crawley 1990). A recent review on restoration ecology in semi-arid environments (Call and Roundy 1991) stressed the importance of understanding the processes involved in seedling establishment. Knowledge of which microhabitats are important is useful since a method of increasing cover of certain species may be to recreate microhabitats which promote recruitment. However, manipulative experiments are needed to test whether seeds are "nursed" or merely "trapped", since the outcome would influence the type of microhabitat required.

6.7 REFERENCES

Beukman,R.P. 1991. The role of nurse plants in the vegetation dynamics of the Succulent Karoo. Master of Science Thesis, Botany Department, University of Cape Town.

Call,C.A. and Roundy,B.A. 1991. Perspectives and processes in revegetation of arid and semi-arid rangelands. Journal of Range Management 44:543-549.

Castellanos,A.E. and Molina,F.E. 1990. Differential survivorship and establishment in Simmondsia chinensis (Jojoba). Journal of Arid Environments 19:65-76.

Crawley,M.J. 1990. The population dynamics of plants. Philosophical Transactions of the Royal Society of London 330:125-140.

Crisp,M.D. 1978. Demography and survival under grazing of three Australian semi-arid shrubs. Oikos 30:520-528.

Dean,W.R.J. and Milton,S.J. 1991. Disturbances in semi-arid shrubland and arid grassland in the Karoo, South Africa: mammal diggings as germination sites. African Journal of Ecology 29:11-16.

Dean,W.R.J. and Yeaton,R.I. 1992. The importance of harvester ant Messor capensis nest-mounds as germination sites in the southern Karoo, South Africa. African Journal of Ecology 30:335-345.

Ellis,F. and Lambrechts,J.J.N. 1986. Soils. In: The Karoo biome: a preliminary synthesis. Part 1. - physical environment, eds. R.M. Cowling, P.W. Roux and A.J.H. Pieterse. South African National Scientific Programmes Report No. 124, Council for Scientific and Industrial Research, Pretoria. pp 18-38.

Facelli,J.M. and Pickett,S.T.A. 1991. Plant litter: its dynamics and effects on plant community structure. Botanical review 57:1-32.

Fonteyn,P.J. and Mahal,B.E. 1981. An experimental analysis of structure in a desert plant community. Journal of Ecology 69:883-896.

Fowler,N.L. 1986. Microsite requirements for germination and establishment of three grass species. American Midland Naturalist 115:131-145.

Fowler,N.L. 1988. What is a safe site?: neighbour, litter, germination date, and patch effects. Ecology 69:947-961.

Grubb,P.J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. Biological review 52:107-145.

Harper,J.L. 1977. Population Biology of Plants. Academic press, New York. 892pp.

Henrici,J.M. 1935. Germination of karoo bush seeds. South African Journal of Science 32:223-234.

Henrici,J.M. 1939. Germination of karoo bush seeds. South African Journal of Science 36:212-219.

Hoffman,M.T. 1989. A preliminary investigation of the phenology of subtropical thicket and Karroid shrubland in the lower Sundays river valley, S.E. Cape. South African Journal of Botany 55:586-597.

Hoffman,M.T. and Cowling,R.M. 1987. Plant physiognomy, phenology and demography. In: The Karoo biome: a preliminary synthesis. Part 2. - vegetation and history, eds. R.M. Cowling and P.W. Roux. South African National Scientific Programmes Report No. 142, Council for Scientific and

Industrial Research, Pretoria. pp 1-34.

Jordaan,P.W. and Nobel,P.S. 1979. Infrequent establishment of seedlings of Agave deserti (Agavaceae) in the northwestern Sonoran desert. American Journal of Botany 66:1079-1084.

Jordaan,P.W. and Nobel,P.S. 1982. Height distributions of two species of cacti in relation to rainfall, seedling establishment and growth. Botanical Gazette 143:511-517.

Lovegrove,B.G. and Siegfried,W.R. 1986. The distribution and formation of mima-like earth mounds in the western Cape region of South Africa. South African Journal of Science 82:432-436.

McAuliffe,J.R. 1986. Herbivore-limited establishment of a Sonoran desert tree Cericidium microphyllum. Ecology 67:276-280.

McAuliffe,J.R. 1988. Markovian dynamics of simple and complex desert plant communities. The American Naturalist 131:459-490.

Milton,S.J. 1992. Effects of rainfall, competition and grazing on flowering of Osteospermum sinuatum (Asteraceae) in arid karoo rangeland. Journal of the Grassland Society of South Africa 9:158-164.

Milton,S.J. and Dean,W.R.J. 1990. Seed production in rangelands of the southern Karoo. South African Journal of Science 86:231-233.

Milton,S.J., Dean,W.R.J. and Kerley,G.I.H. 1992. Tierberg Karoo Research Centre: history, physical environment, flora and fauna. Transactions of the Royal Society of southern Africa 48:15-46.

Noble,I.R. and Crisp,M.D. 1980. Germination and growth models of short-lived

grass and forb populations based on long term photo-point data at Koonamore, South Australia. Israel Journal of Botany 28:195-210.

Noy-Meir,I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4:25-51.

Owens,M.K. and Norton,B.E. 1989. The impact of "available area" on Artemisia tridentata seedling dynamics. Vegetatio 82:155-162.

Parker,M.A. 1982. Association with mature plants protects seedlings from predation in an arid grassland shrub, Gutierrezia microcephala. Oecologia 53:276-280.

Roux,P.W. 1968. Veld management in the Karoo and adjacent sweet grassveld regions. In: Small stock industry in South Africa, ed. W.J. Hugo. Government Printer, Pretoria. pp 318-340.

Rutherford,M.C. and Westfall,R.H. 1986. Biomes of southern Africa - an objective categorisation. Memoirs of the Botanical Survey of Southern Africa 54:45-65.

Sala,O.E. and Lauenroth,W.K. 1982. Small rainfall events: an ecological role in semi-arid regions. Oecologia 53:301-304.

Sherbrook,W.C. 1977. First year seedling survival of Jojoba (Simmondsia chinensis) in the Tuscon mountains, Arizona. The South Western Naturalist 22:225-234.

Soriano,A. and Sala,O.E. 1986. Emergence and survival of Bromus setifolius seedlings in different microsites of a Patagonian arid steppe. Israel Journal of Botany 35:91-100.

Steenbergh,W.F. and Lowe,C.H. 1969. Critical factors during the first years of life of the Saguaro (Cereus giganteus) at Saguaro National Monument, Arizona. Ecology 50:826-834.

Tidmarsh,C.E.M. and Havenga,C.M. 1955. The wheel-point method of survey and measurement of semi-open grasslands and karoo vegetation in South Africa. Memoirs of the Botanical Survey of South Africa No. 29, Government Printers, Pretoria.

Turner,R.M., Alcorn,S.M., Olin,G. and Booth,J.A. 1966. The influence of shade, soil and water on saguaro seedling establishment. Botanical Gazette 127:95-102.

Turner,R.M., Alcorn,S.M. and Olin,G. 1969. Mortality of transplanted saguaro seedlings. Ecology 50:835-844.

Vidella,P.E. and Armesto,J.J. 1989. Emergence of ephemeral plant species from soil samples of the Chilean Coastal desert in response to experimental irrigation. Revista Chilena de Historia Natural 62:99-107.

Went,F.W. 1942. The dependence of certain annual plants on shrubs in the southern California desert. Bulletin of the Torey Botanical Club 69:100-114.

Went,F.W. 1949. The effects of rain and temperature on plant distribution in the desert. Research Council of Israel Special Publication No. 2, Desert Research. pp 230-240.

Westoby,M. 1980. Elements of a theory of vegetation dynamics in arid rangelands. Israel Journal of Botany 28:169-194.

Yeaton,R.I. and Esler,K.J. 1990. The dynamics of a succulent karoo vegetation: a study of species association and recruitment. Vegetatio 88:103-113.

CHAPTER 7

EXPERIMENTAL EFFECTS OF WATER STRESS ON SEMI-ARID KAROO SEEDLINGS: IMPLICATIONS FOR FIELD SEEDLING SURVIVORSHIP

Submitted as Esler,K.J. and Phillips,N., Journal of Arid Environments

7.1 ABSTRACT

Very little is known about seedling establishment in the semi-arid Karoo of southern Africa. In a greenhouse study, the responses of seedlings of three shrub species to water stress were investigated by withholding water at different stages of seedling development. Mortality of the two Asteraceous species, Pteronia pallens L.F. and Osteospermum sinuatum (D.C.) T.Norl. was more rapid where seedlings were provided with water for longer periods before being subjected to water stress. Hardened seedlings, exposed to water stress at an earlier stage, survived the longest. These seedlings were the smallest with respect to root and shoot mass. Seedlings of the leaf succulent Ruschia spinosa (L.) H.E.K. Hartm. & Stuber. were extremely hardy and after 400 days without water, approximately 80% of the seedlings were still alive. The last P. pallens seedling died 160 days after water had been withheld. O. sinuatum seedlings were the least tolerant to water stress and 100% mortality occurred within 120 days. These results are discussed in terms of microhabitat preferences of the seedlings in field situations.

7.2 INTRODUCTION

Owing to the slow rate of population change and the logistical difficulties involved in undertaking long-term monitoring, very little is known about the performance of seedlings in semi-arid shrublands. In these areas, rainfall events are spatially and temporally variable, and prolonged droughts are a common factor influencing plant physiology and ecology (Westoby 1980). Seedlings are especially vulnerable to water stress, and germination and recruitment are thought to be critical stages in the life cycles of many semi-arid plants. Although a minimum amount of rain may be required for a germination event (Vidiella and Armesto 1989), seedling survival depends on adequate post-germination rainfall (Steenbergh and Lowe 1969, Jordan and Nobel 1982, Castellanos and Molina 1990). The timing and amount of rainfall is not always predictable (Westoby 1980).

An understanding of seedling responses to water scarcity provides some insight into restoration management problems. For example, information on differential survival characteristics of seedlings can be used to assist in the selection of species for re-introduction into disturbed vegetation. Furthermore, an understanding of the mechanism and rates of recruitment is important for managers, since these processes influence population turnover and therefore maintenance of cover.

In the Karoo, a large semi-arid rangeland covering approximately 33% of South Africa's land surface (Rutherford and Westfall 1986), summer drought is common (Booysen and Rowswell 1983, Werger 1986). Large soil and/or canopy seed banks are not characteristic of perennials in this environment (Chapters 4 and 5) and after sufficient rainfall, recruitment events take place provided seeds are available (Chapter 6). Data from Australian (Crisp 1978) and North American semi-arid regions (Turner et al. 1966, Turner et al. 1969, Steenbergh and Lowe 1969, Castellanos and Molina 1990) suggests that mortality rates in juvenile plants are very high. Field observations in the southwestern part of the Great Karoo (on the farm Tierberg) confirm this (Chapter 6). Herbivory and water stress have been

highlighted as being the greatest sources of this mortality (Steenbergh and Lowe 1969, Turner et al. 1969) and recruitment patterns are often reflected in adult-plant age structure (Jordaan and Nobel 1982).

This study focused on three relatively common perennial species from the southwestern part of the Great Karoo, near Prince Albert (33°10'S, 22°17'E). The responses of seedlings of these species to water stress were investigatied in a greenhouse environment by withholding water from seedlings at different stages of development. Greenhouse studies on the emergence and survival of grass seedlings in relation to wet-dry sequences have shown that seedlings often fail to survive after germination because inadequate soil water limits the development of root systems capable of supporting the plant through drought (Frasier et al. 1984, 1985). It was predicted, therefore, that seedling mortality would be lower for seedlings subjected to longer periods of moisture prior to drought, since they would have developed extensive root systems.

Although greenhouse studies cannot duplicate field conditions, they do provide information on the broad range of responses of species to water scarcity. In this chapter, the results are discussed in terms of microhabitat preferences of the seedlings in an attempt to bridge the gap between experimental and field conditions.

7.3 METHODS AND MATERIALS

7.3.1 Study site and study species

Ruschia spinosa (L.) H.E.K. Hartm. & Stuber., Pteronia pallens L.f. and Osteospermum sinuatum (DC.) T. Norl. are co-dominants on the plains of the Tierberg study site near Prince Albert in the Succulent Karoo (33°10'S, 22°17'E). Vegetation on the plains is relatively homogeneous, comprising perennial succulent (mostly Mesembryanthema in the Aizoaceae) and non-succulent (mostly Aster-

aceae) shrubs. The plains comprise approximately 78% of the 100 ha study site (Milton et al. 1992), the rest of the area being occupied by mima-like mounds, or *heuweltjies* (Lovegrove and Siegfried 1986) and drainage lines. Descriptive data on each of the three study species are provided in Table 7-1. All three species are common on the study site and are considered to play a role in the dynamics of the system (Yeaton and Esler 1990).

Table 7-1. Descriptive data on each of the three study species from the farm Tierberg in the Karoo. Density, moisture content and seed production data are means ± standard errors.

	Pteronia pallens	**Osteospermum sinuatum**	**Ruschia spinosa**
Family	Asteraceae	Asteraceae	Aizoaceae
Palatability[a]	unpalatable	palatable	unpalatable
Structural attributes	evergreen non-succulent woody	deciduous non-succulent woody	evergreen leaf-succulent woody
Plant height	40-70cm	10-50cm	10-40cm
Density/100m^2 [b]	30 ± 22	65 ± 4	62 ± 7
% Moisture content of above ground parts [c]	28.7 ± 5.2	59.6 ± 4.1	58.3 ± 8.7
Canopy volume (CC x 10^{-3})[b]	104.0 ± 11.1	91 ± 1.2	-
Seed production per m^2 [b]	60	66	107

[a] = palatability to livestock (sheep).
[b] = data for Tierberg from Milton (1990).
[c] = data for Tierberg from Milton and Dean (1990).

The study site receives approximately 170 mm of rain per annum, falling mostly in autumn (March-May) and spring (September-November) (Milton et al. 1992). The most predictable rains occur between March and May, coinciding with the ripening of seed. This period appears to be an important time for germination

(Chapter 6). Droughts lasting a month or longer often occur between September and January (Milton et al. 1992). Seedlings are therefore subjected to a very harsh environment after recruitment. Temperatures at the study site range from -5°C (winter minimum) to 43°C (summer maximum) with a mean annual temperature of 17.5°C (Milton et al. 1992).

7.3.2 Greenhouse experiment

The seedling water stress experiment was undertaken at the Elsenberg Agricultural College, Stellenbosch (33°55'S, 18°52'E), in glass houses. These were not temperature controlled and temperature fluctuations reflected ambient conditions. Temperatures at Stellenbosch are considerably less extreme than Karoo field situations. Humidity in the enclosures was generally higher than field humidities due to circulation of air through a water cooled air conditioner designed to offset increased glass house temperatures.

Seed of P. pallens and R. spinosa was collected during January 1990 from the Tierberg study site. Seed of O. sinuatum was obtained from the Worcester Veld Reserve in the Karoo (33°39'S, 19°26'E) where plants are grown for seed production. Seed of this species is immediately dispersed on ripening and is therefore difficult to collect in the field.

Seed was sown into pots containing approximately five litres of soil. Pot soil comprised 1 portion compost: 2 portions study site soil: 4 portions pasteurised river sand. The pot soil medium was standardised by using soil collected from the Tierberg study site but to alleviate soil compaction and to increase drainage, pasteurised river sand was added. Compost was added to adjust for nutrient loss due to dilution of the field-collected soil. Comparative results of soil analyses for pot and study site soil are presented in Table 7-2.

Pot and dry soil weights were recorded at the beginning of the experiment. This enabled the gravimetric determination of the percentage water content of each pot.

Soil water retention curves were determined for pot and field collected soil using a pressure plate apparatus to a soil water potential of -1.5 MPa. This procedure links gravimetric soil water content to matric soil water potential.

Seed of P. pallens was sown on 23 March 1990 and began germinating on 27 March 1990. Seedlings were thinned out to an average of 6 per pot. R. spinosa seed was sown on 24 March 1990 and germinated from 26 March 1990. Seedlings of the species were thinned out to an average of 10 per pot. For the above two species, 100 to 120 seedlings were used in each treatment. Very few O. sinuatum seedlings germinated and no thinning was necessary (an average of one seedling per pot). Seedlings were sown on 19 June 1990 and began germinating from 28 June 1990. Approximately 50 seedlings were used per treatment due to the poor germination success.

All pots were given 500 ml of water per day until the start of each treatment. Control pots were watered every day. In each treatment, water was withheld from the seedlings at a different stage of development (Table 7-3). Treatments were initiated at the cotyledon stage (treatment 1, T1), first leaf pair (treatment 2, T2), second leaf pair (treatment 3, T3) and third leaf pair (treatment 4, T4) stages, but due to the slow loss of pot water, seedlings did not immediately experience water stress. Seedlings at the cotyledon stage were therefore not exposed to water scarcity. At regular intervals throughout the experiment, the number of surviving seedlings were counted (seedlings were considered dead when no more green material was obvious, i.e. they were no longer able to photosynthesise). To allow for comparisons between treatments, data were converted to percent seedling survivorship. Seedling death rates were assumed to be independent of temperatures in the greenhouse environment and treatment initiation was regarded as day 1 for all treatments. This allowed the differences between curves to be tested as if they began on the same day. The Kolmogorov-Smirnov two sample test (Siegel 1956) was used to determine differences in the percentage survivorship curves, over time, of seedlings under different treatments for P. pallens and O. sinuatum. This test could not be conducted on R. spinosa seedling survivorship data as the

experiment was terminated before 100% mortality (Pyke and Thompson 1986). However, a Chi-squared test (Zar 1984) on the proportion of seedlings surviving in each treatment was used as a test of significance.

Root to shoot ratios, stomatal counts and relative water content studies were determined for P. pallens and R. spinosa. There were too few replicates of O. sinuatum for this purpose. Stomatal counts were conducted by obtaining epidermal impressions using clear nail varnish. The stomatal "templates" were counted under 400x magnification. Both the adaxial and abaxial surfaces of the P. pallens leaves were sampled, and only the lateral, side surface of the R. spinosa leaves were sampled (i.e. exposed surface). Stomatal counts were conducted on control and T1 plants.

To relate the experimental results to the field situation, a rainfall simulation programme, GENRAIN (Zucchini and Adamson 1984) was used to generate field rainfall patterns. This programme uses rainfall records from existing weather stations to generate artificial rainfall sequences. The closest weather station to the study site was Zachariasfontein, 14 km North West of Tierberg (33°5'S, 22°0'E). It was assumed that rainfall patterns at this station were similar to those at Tierberg. Five hundred years of artificial rainfall sequences were generated for this station. Any rainfall events greater than 10 mm were regarded as being significant (Sala and Lauenroth 1982). These data were then used to generate probabilities of there being ten or more rain free days between rainfall events greater than 10 mm.

7.4 RESULTS

A soil water potential of -1.5 MPa, the conventional norm for the permanent wilting point of most crop plants (Slatyer 1967), occurred at a gravimetric water content of 3.5% for pot soil and 6.5% for field collected soil. The permanent

wilting point for pot soil occurred at a lower gravimetric soil water content, probably due to the addition of sand which increased drainage.

In all three species, T1 plants (those exposed to water stress for the longest) were the smallest in size and T4 plants were the largest (personal observation; Table 7-4: number of Ruschia spinosa leaf pairs). Data for R. spinosa and Pteronia pallens indicated that T1 seedlings were the smallest in shoot and root mass, whilst T4 seedlings were the largest (Table 7-5).

Loss of soil pot water occurred at the same rate in all Pteronia pallens treatments (Fig. 7-1b). The permanent wilting point of -1.5 MPa was reached at day 35 (Fig. 7-1b). Kolmogorov-Smirnov two sample tests indicated significant differences ($P \leq 0.001$) in seedling mortality between each combination of treatments. Seedlings that were water stressed at an earlier stage (T1) survived the longest (Fig. 7-1a). T1 seedlings of P. pallens survived approximately 2 months after the pot soil had reached the agricultural wilting point (Fig. 7-1a). Mortality of seedlings that were given more water for longer at an earlier stage of development (T3, T4) began soon after the agricultural wilting point of the soil was reached (Figs. 7-1a, 7-1b). A t-test indicated that there was a significant difference in the number of stomata on the adaxial leaf surfaces between P. pallens control and T1 plants ($t = 4.911$, $P < 0.05$, d.f. = 40, Table 7-6). Stomatal numbers were reduced in the T1 plants. No significant differences between treatments were found for the number of stomata on the abaxial leaf surfaces (Table 7-6). Results for shoot to root ratios in P. pallens were inconclusive (Table 7-4). Although an analysis of variance (ANOVA) indicated significant differences between treatments (F-ratio = 2.994, $P < 0.05$, d.f = 4,43), a multiple range test showed no difference between treatments (Table 7-4). Shoot relative water contents were significantly different between treatments (ANOVA: F-ratio = 100.151, $P < 0.001$, d.f. = 4,44), with control and T4 plants being more turgid (Table 7-5). Trends were not as clear in root relative water contents and root and shoot dry weights.

Pot soil water loss did not occur at the same rate for all of the Osteospermum sinuatum treatments (Fig. 7-2b). It is possible that the larger leaf mass of the T3 seedlings (personal observation) resulted in an increased rate of pot soil water loss through transpiration. The rate of water loss for pots in T3 was more rapid, thus the agricultural wilting point was reached earlier. Figure 7-2a indicates the decline of seedling survivorship of O. sinuatum over time. Kolmogorov-Smirnov two sample tests indicated significant differences ($P \leq 0.001$) between each combination of treatments. As for P. pallens, the seedlings that were water stressed the earliest survived the longest, approximately 25 days after the agricultural wilting point was reached. Seedlings that were provided with water for longer periods (T2, T3) were not as hardy, and death occurred earlier after stressing. The decline in seedling numbers coincided with the pot soils reaching the agricultural wilting points.

Ruschia spinosa seedlings were the most hardy of the three species. Seedling mortality occurred at a very slow rate (Fig. 7-3b) and after approximately 400 days without water, more than 70% of the seedlings were still alive. In contrast with the other two species, no significant differences in rates of seedling mortality were observed between treatments ($\chi^2 = 4.491$, d.f. = 3, non-significant). There were no significant differences between the control and T1 plants with respect to lateral leaf face stomatal counts (Table 7-6). The most obvious effect of the different drought treatments was on the size of the plants. T1 seedlings had significantly fewer leaf pairs compared to the other treatments (ANOVA: F-ratio = 12.941, $P < 0.01$, d.f. = 4,38)(Table 7-4). An ANOVA and a Tukey multiple range test indicated that there were no significant differences in shoot:root ratios between treatments for R. spinosa seedlings (Table 7-4). There were, however, significant differences in shoot and root relative water contents between treatments (ANOVA: shoot F-ratio = 11.03, $P < 0.001$, d.f = 4,39; root F-ratio = 19.167, $P < 0.001$, d.f. = 4,36), with the control and T4 seedlings being more turgid (Table 7-5).

The artificial rainfall sequences generated for Zachariasfontein indicated that there was a 50% probability of getting up to 25 rain free days after a significant (> 10 mm) rain event (Fig. 7-4). As the number of rain free days following a significant rain event increased, the probabilities of these events occurring decreased rapidly.

Table 7-2. Soil physical and chemical data from a) Tierberg study site soil (n = 27, Chapter 2) and b) Pot soil (n = 1). - indicates missing data. * = measurements in $\mu g\ g^{-1}$

	a) Study site soil		b) Pot soil
Variable	**mean**	**s.d.**	
pH	5.59	0.94	6.80
resistance	8.82	4.54	-
Phosphorus*	107.22	99.65	-
Potassium*	130.78	37.40	176.00
Sodium*	157.22	78.58	148.00
Calcium*	5.03	2.84	4.09
Magnesium*	3.07	0.93	2.13
Copper*	1.01	0.23	0.74
Zinc*	1.50	1.25	6.34
Manganese*	132.82	55.18	56.76
Boron*	0.39	0.15	0.44
% Nitrogen	3.98	0.46	3.50
% Silt	11.56	5.40	4.00
% Clay	14.22	8.08	6.00
% Coarse sand	42.72	5.35	61.58
% Medium sand	14.83	2.18	19.30
% Fine sand	16.70	4.18	9.12

Table 7-3. Age of seedlings in days when treatments 1,2,3 and 4 (T1, T2, T3, T4) were initiated (i.e. water was witheld) for each species, and sample size (number of seedlings), given in parentheses for each treatment (C = control).

	Pteronia	Osteospermum	Ruschia
T1	10 (105)	8 (39)	7 (124)
T2	17 (109)	23 (50)	14 (112)
T3	24 (104)	58 (51)	39 (114)
T4	49 (120)	-	51 (120)
C	- (136)	- (59)	- (166)

Table 7-4. a) Number of Ruschia spinosa leaf pairs of same aged seedlings under different water stress treatments and b) shoot to root ratios for R. spinosa and Pteronia pallens. Data are means ± standard deviations. One way analyses of variance were conducted on the data, * = $P < 0.05$, ** = $P < 0.01$, N.S. non-significant. Superscripts indicate results of Tukey multiple range tests. T1-T4 = treatments 1 to 4.

	a)	b)	
	# Ruschia leaf pairs	Ruschia Shoot:Root ratio	Pteronia Shoot:Root ratio
T1	7.1 ± 2.42^{a}	7.24 ± 1.29^{a}	3.05 ± 1.50^{a}
T2	10.44 ± 4.77^{a}	7.14 ± 1.06^{a}	4.67 ± 1.58^{a}
T3	12.75 ± 3.58^{ab}	6.09 ± 1.34^{a}	4.79 ± 1.59^{a}
T4	19.75 ± 7.61^{bc}	5.99 ± 1.97^{a}	4.99 ± 1.38^{a}
Control	22.75 ± 7.13^{c}	5.57 ± 1.01^{a}	4.86 ± 1.40^{a}
Sig.	0.01	N.S.	0.05

Table 7-5. a) Relative water content and b) Dry weight (grams) of Ruschia spinosa and Pteronia pallens seedlings from different water stress treatments (T1, T2, T3, T4, Control). Data are means ± standard deviations. One way analyses of variance were conducted on the data, * = $P < 0.05$, *** = $P < 0.001$, N.S. = non-significant. Superscripts indicate results of Tukey multiple range tests. T1 - T4 = treatments 1 to 4, C = Control.

	Ruschia spinosa		Pteronia pallens	
a) Relative water content				
	Shoot	Root	Shoot	Root
T1	61.81 ± 8.01^{a}	73.42 ± 6.54^{a}	43.91 ± 7.82^{a}	77.22 ± 28.82^{b}
T2	63.64 ± 10.34^{ab}	64.81 ± 5.16^{ab}	46.92 ± 9.24^{a}	71.09 ± 10.03^{ab}
T3	74.68 ± 8.33^{bc}	70.16 ± 11.02^{ab}	51.32 ± 4.70^{a}	63.57 ± 3.26^{ab}
T4	77.31 ± 9.29^{c}	74.19 ± 5.50^{b}	83.99 ± 2.65^{b}	52.99 ± 2.54^{a}
C	84.20 ± 4.92^{c}	93.78 ± 1.72^{c}	85.79 ± 4.53^{b}	102.25 ± 12.53^{c}
Sig.	***	***	***	***
b) Dry weight (grams)				
T1	0.10 ± 0.04^{a}	0.01 ± 0.00^{a}	0.04 ± 0.02^{a}	0.02 ± 0.01^{a}
T2	0.17 ± 0.08^{a}	0.02 ± 0.01^{a}	0.10 ± 0.07^{ab}	0.02 ± 0.02^{a}
T3	0.21 ± 0.05^{ab}	0.03 ± 0.01^{a}	0.09 ± 0.07^{ab}	0.02 ± 0.01^{a}
T4	0.30 ± 0.12^{b}	0.05 ± 0.02^{a}	0.15 ± 0.14^{b}	0.03 ± 0.02^{a}
C	0.33 ± 0.12^{b}	0.16 ± 0.28^{a}	0.14 ± 0.09^{ab}	0.03 ± 0.02^{a}
Sig.	***	N.S.	*	N.S.

Table 7-6. Mean number of stomata ± standard deviations under 400x magnification on leaves of Pteronia pallens (adaxial and abaxial surfaces) and Ruschia spinosa (exposed, lateral leaf surface). Control seedlings had recieved daily watering whilst treatment 1 (T1) seedlings had water withheld from them since the cotyledon stage. T-tests were conducted on the data, * = $P < 0.05$, N.S. = non-significant. Sample sizes are given in parentheses.

	Control	T1	Sig.
Pteronia adaxial	14.18 ± 1.63 (17)	10.95 ± 2.35 (25)	*
Pteronia abaxial	17.15 ± 2.98 (27)	16.95 ± 2.12 (22)	N.S.
Ruschia lateral	7.93 ± 2.10 (29)	7.03 ± 2.54 (30)	N.S.

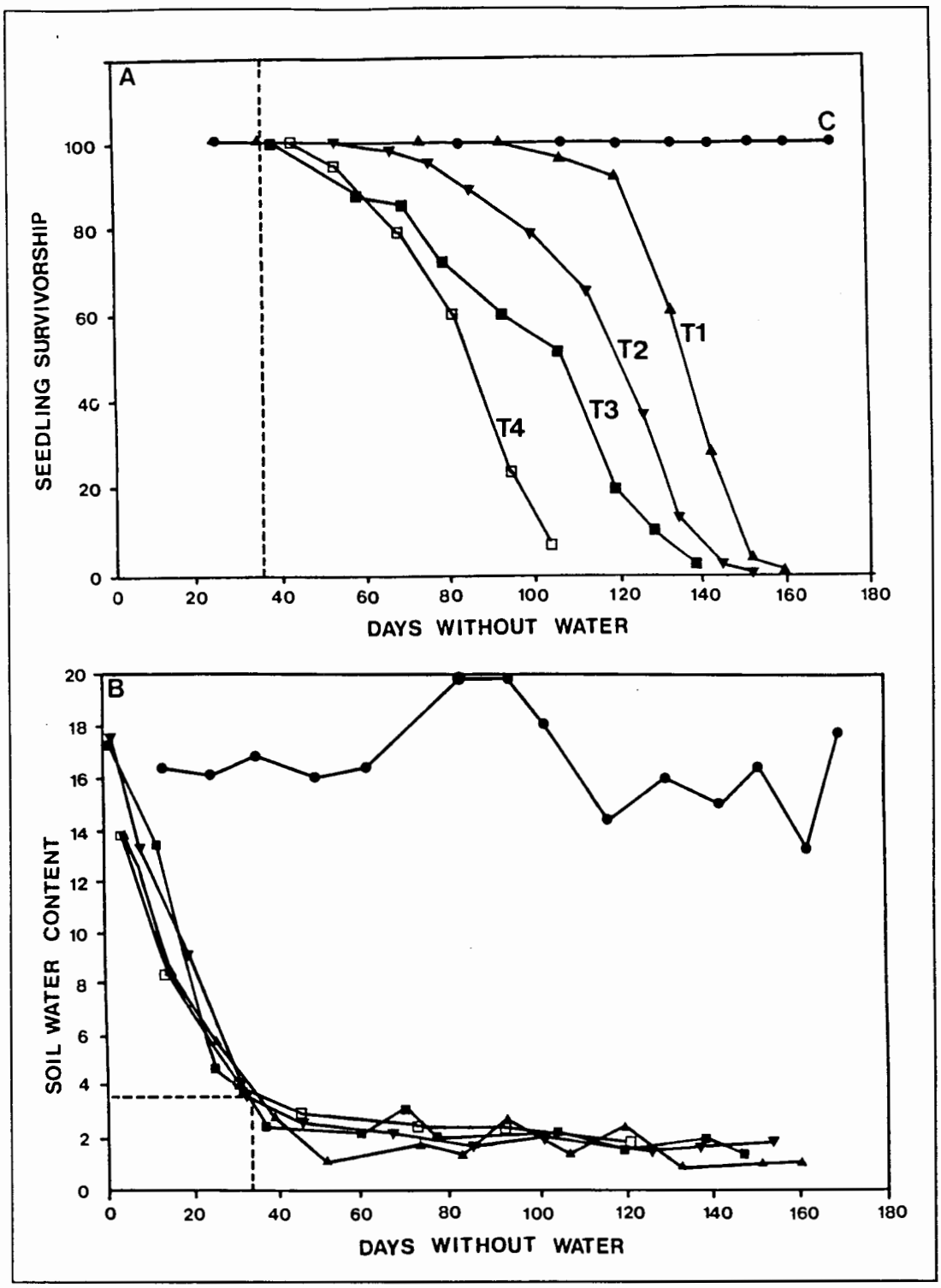

Figure 7-1. a): Pteronia pallens seedling survivorship over time (days without water). Control: continuous watering. Treatments: Water was withheld at the following times: T1 = 10 day old seedlings, cotyledon stage; T2 = 17 day old seedlings, 1st leaf pair stage; T3 = 24 day old seedlings, 2nd leaf pair stage; T4 = 49 day old seedlings, three or more leaf pairs.
b): Pteronia pallens percentage pot soil water content (gravimetrically determined) over time (days since treatment initiation). -- = - 1·5 MPA.

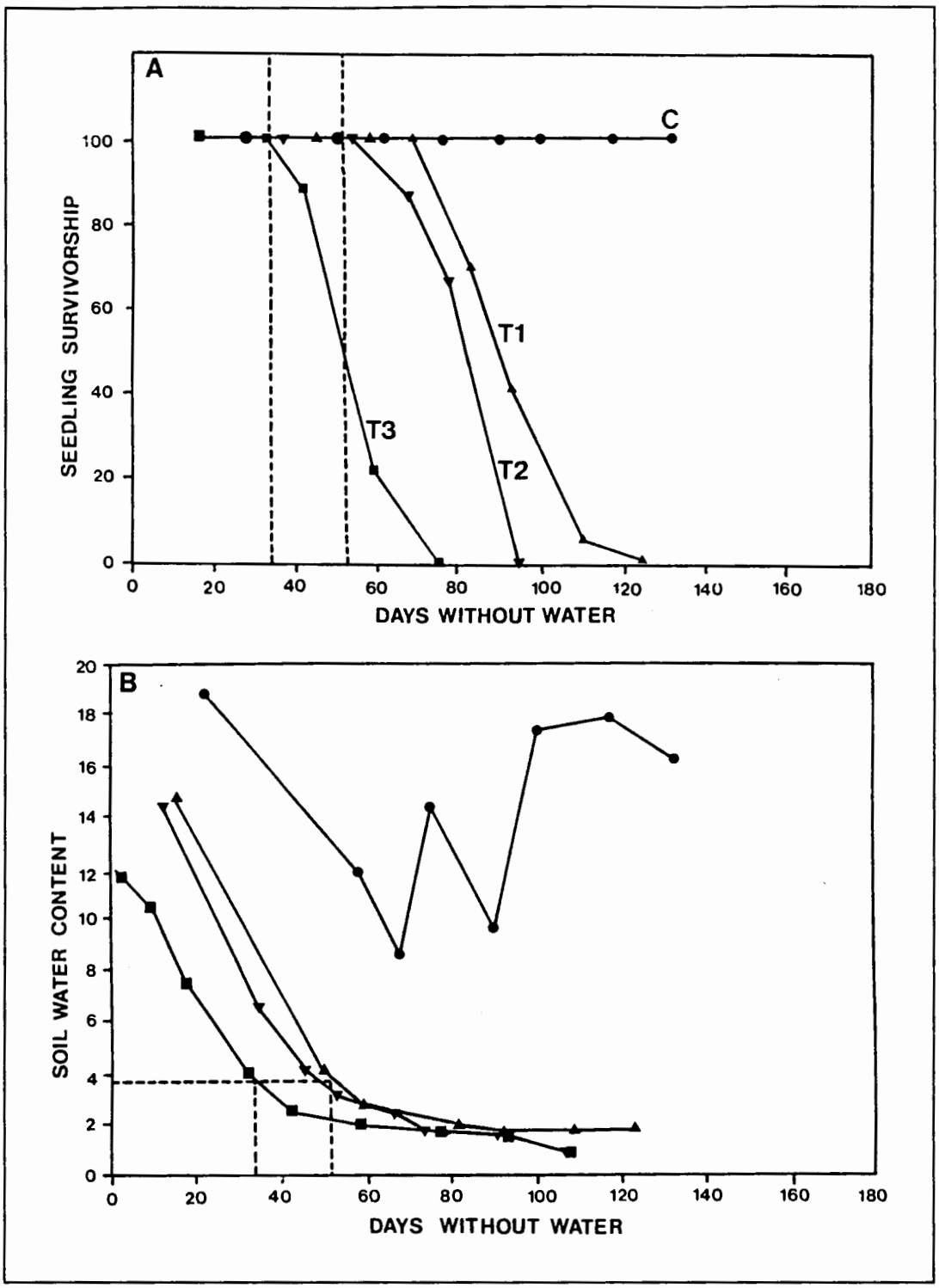

Figure 7-2. a): Osteospermum sinuatum: percentage seedling survivorship over time (days without water). Control: continuous watering. Treatments: Water was withheld at the following times: T1 = 8 day old seedlings, cotyledon stage; T2 = 23 day old seedlings, 3rd leaf pair stage; T3 = 58 day old seedlings. b): Osteospermum sinuatum percentage pot soil water content (gravimetrically determined) over time (days since treatment initiation). **-- = −1·5 MPA.**

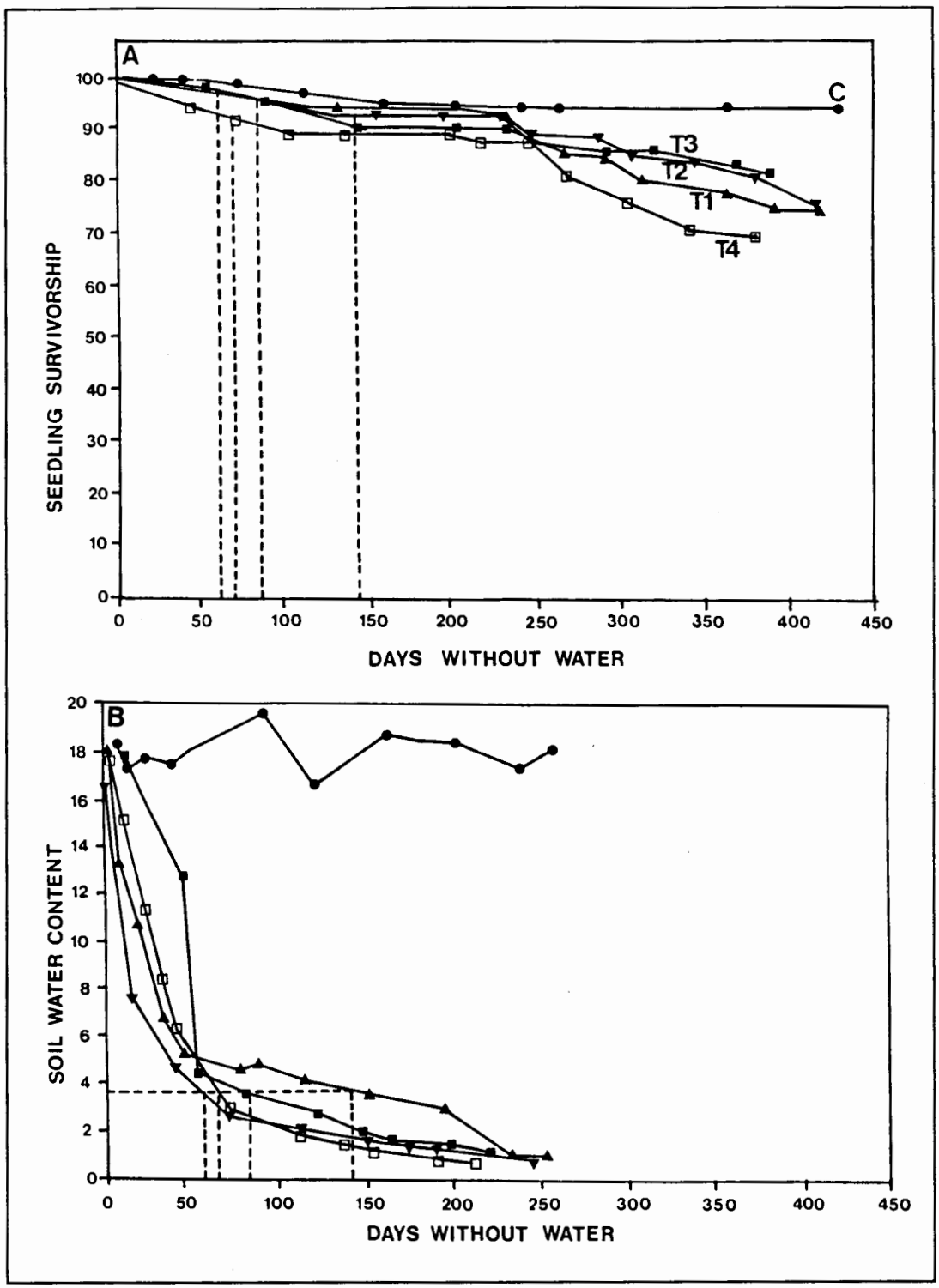

Figure 7-3. a): Ruschia spinosa: percentage seedling survivorship over time (days without water). Control: continuous watering. Treatments: Water was withheld at the following times: T1 = 7 day old seedlings; T2 = 14 day old seedlings; T3 = 39 day old seedlings; T4 = 51 day old seedlings. b): Ruschia spinosa percentage pot soil water content (gravimetrically determined) over time (days since treatment initiation). **--= -1·5 MPA.**

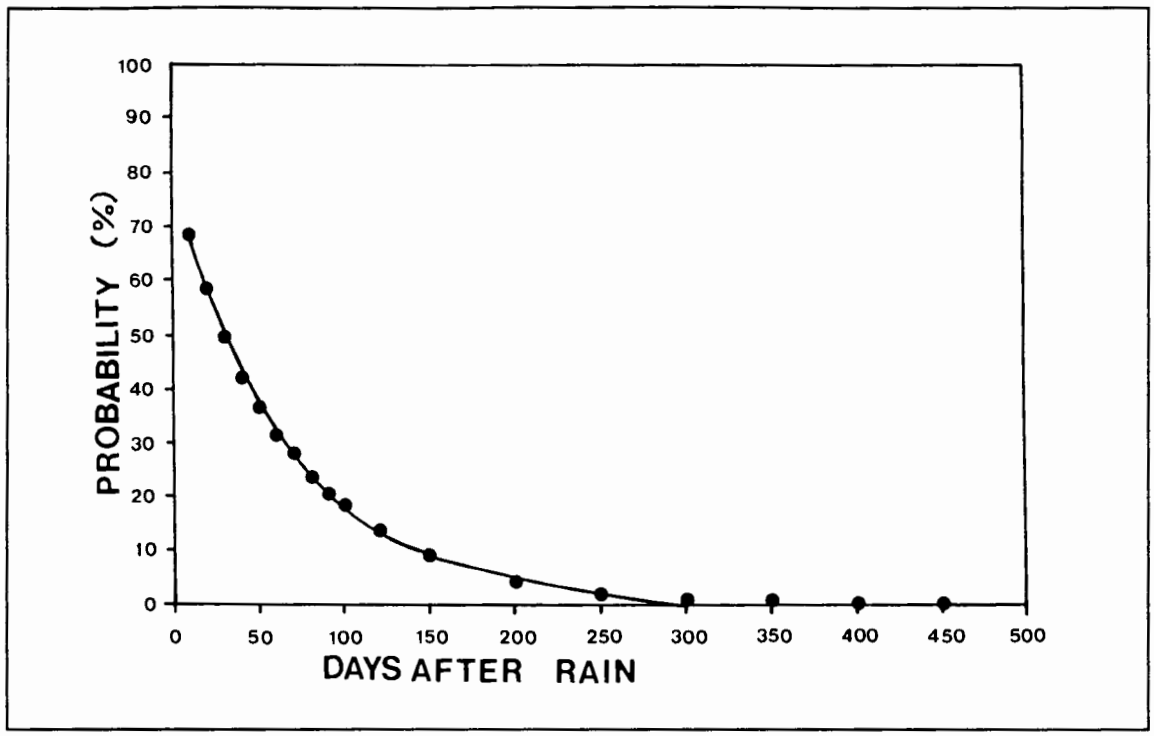

Figure 7-4. Probability of getting X or more rain free days between rainfall events of 10 mm or greater. Probabilities obtained using the rainfall simulation programme GENRAIN (Zucchini and Adamson 1984).

7.5 DISCUSSION

7.5.1 Between treatment variation

The seedlings of the two Asteraceous species Pteronia pallens and Osteospermum sinuatum reacted in a similar way when subjected to water stress. In both species, seedlings exposed to water stress at an earlier stage (i.e. youngest seedlings, T1) survived the longest (Figs. 7-1b, 7-2b). Mortality was more rapid in those seedlings which were provided with water for a longer period before being deprived of water (T3, T4). In semi-arid environments, where rainfall is variable and low, this "hardening" effect (or merely a plant size effect) would appear to have some advantage. Soriano and Sala (1986) noted seedling survivorship through a summer drought in a Patagonian semi-arid shrub steppe. Young plants in fully exposed "harsher" environments showed higher survival rates than plants establishing beneath shrubs. The smaller ratios of shoot length to root length, resulting in more efficient water use, was cited as being the major factor influencing this pattern. Although the results for P. pallens were inconclusive with respect to shoot:root ratios, the trend was for lower ratios to be found in seedlings exposed to water stress for longer periods (Soriano and Sala 1986). Stomatal counts indicated that there were significantly more stomata on the adaxial leaf surfaces of control plants as compared to T1 plants (Table 7-6). These results could not be accounted for by leaf turgidity as control plants were more turgid (Table 7-5). It is possible that the reduction in the number of stomata in "hardened" seedlings is a developmental attribute of the seedlings; however, this needs more investigation. Overall plant size was certainly influenced by drought treatments (Table 7-5). Seedlings that were provided with more than 10 days of watering before treatment initiation grew rapidly and at the onset of water stress had greater leaf surface areas. It is unlikely that seedlings will receive more than ten days of rainfall in the natural environment (significant rainfall events are usually followed by rain free days, Fig. 7-4), however soil could remain saturated for a length of time after a heavy rainfall event. T1 seedlings received a watering regime which more closely approximated natural conditions. Growth rates were slow,

resulting in smaller "hardened" seedlings. Slower growth rates and resulting smaller leaf surface areas are advantageous for seedlings in areas where there is a high probability of water stress after a germination event. In the field, seedlings must endure summer conditions of prolonged rain free periods combined with high temperatures.

No significant mortality was recorded for all Ruschia spinosa treatments, moreover, there were no significant trends between treatments with respect to shoot:root ratios and stomatal counts. This result is interesting when compared to the findings of Von Willert et al. (1985). They followed the performance of adult species of Mesembryanthema during an extended drought where there were no "significant" rainfall events (>10 mm) for twelve months. During this drought, approximately 80% of the vegetation was killed. It appears that a predictable water supply is a prerequisite for Crassulacean Acid Metabolism (CAM) in the Richtersveld (Namib Desert) (Von Willert et al. 1985). Why then did Ruschia spinosa seedlings cope so well with an extended period of water stress? Firstly, this species has a very wide distribution (unlike many Richtersveld Mesembryanthema which have localised distributions, Jürgens 1986) which indicates that it is tolerant of a wide range of conditions. Secondly, Von Willert et al. (1985) noted that CAM succulents are able to take up atmospheric water vapour. It is possible that the higher humidity in the greenhouse assisted this species, despite low soil water potentials. However, this particular species exhibits very weak CAM (Phillips unpublished data). The ability of this species to tolerate prolonged water stress is probably greater than most full CAM plants.

7.5.2 Between species variation

The results show some interesting differences between species. Seedlings of the succulent Ruschia spinosa were extremely hardy and after 400 days with no water, very little mortality had occurred, regardless of treatment. The last Pteronia pallens seedlings died 160 days after watering ceased. Osteospermum sinuatum seedlings were the least hardy and 100% mortality had occurred after 120 days.

The meaning of these time periods (to 100% mortality) for seedlings of the different species growing in the field was investigated using probabilities extracted from the simulated rainfall data set (Fig. 7-4). This indicated that there was a 58% chance of there being 20 or more rain free days after a significant rainfall event. This figure declined rapidly to an 18% chance of there being 100 or more rain free days after a significant rain event (Fig. 7-4). According to the experimental survivorship data, O. sinuatum, which survived the shortest length of time of the three species (approximately 100 days), would have no problem surviving in the field given only an 18% chance of failure. In reality, mortality in the field is high (Chapter 6). Future experiments should concentrate on the earlier stages of recruitment (i.e. immediately after germination), since these would provide results more applicable to field conditions. Field observations (Chapter 6) indicate that the early seedling stage is an important bottleneck in the population dynamics of these species.

The relative survivorship of the three species should be seen in a field context. In a succession model proposed by Yeaton and Esler (1990) for the Tierberg study site, these species play different roles in the dynamics of the system. Mound-forming species of Mesembryanthema like R. spinosa (= Eberlanzia cf. vulnerans in Yeaton and Esler, 1990) are able to colonise open areas between existing vegetation. These then provide woody shrubs like P. pallens and O. sinuatum with protected sites in which to establish (Yeaton and Esler 1990). These patterns are correlated with the seed and seedling biology of the three species investigated. Both O. sinuatum and P. pallens have seeds which are readily dispersed by wind and consequently seed density low in the open and high under nurse plants (mound-forming Mesembryanthema) and in litter where the seed is trapped after dispersal (Yeaton and Esler 1990, Chapter 6). These species may require "nursing" at the seedling stages, as their ability to survive under extreme water stress is limited. "Nursed" microsites are less extreme than the open sites into which Mesembryanthema species (family Aizoaceae) germinate and recruit (Yeaton and Esler 1990, Chapter 6). Open sites are harsh with respect to temperature and possibly water availability and the ability of R. spinosa seedlings to cope with these

environments is reflected in the experimental results; of the three species studied, R. spinosa seedlings were the most adapted to extreme water stressed conditions. It must be noted however, that dispersal and seed bank data (see Chapters 5 and 6) indicate that "nursing" may be less important than believed in the succession model (Yeaton and Esler 1990). The "nursing" hypothesis requires more detailed field studies of life history patterns, physiological differentiation and dispersal characteristics of the species involved.

Finally, the data do provide some insight into restoration management problems. Osteospermum sinuatum is a palatable perennial shrub of great interest to stock farmers. As a result of overgrazing, the abundance of this species is very low in many parts of the Karoo and attempts have been made to re-introduce the species into some areas (Joubert and Van Breda 1976). The data indicates that O. sinuatum seedlings are unlikely to survive in open areas. If one wished to reintroduce this species into disturbed vegetation, artificial microsites would have to be provided (be it for "trapping" seeds or "nursing" seedlings). Alternatively, the vegetation could be reseeded sequentially (bearing in mind the successional sequence proposed by Yeaton and Esler 1990); R. spinosa seedlings are tolerant of harsh conditions, and the adult plants of this species may provide sheltered microsites which enable recruitment of species (Yeaton and Esler 1990) like O. sinuatum.

7.6 REFERENCES

Booysen,J. and Rowswell,D.I. 1983. The drought problem in the Karoo areas. Proceedings of the Grassland Society of Southern Africa 18:40-45.

Castellanos,A.E. and Molina,F.E. 1990. Differential survivorship and establishment in Simmondsia chinensis (Jojoba). Journal of Arid Environments 19:65-76.

Crisp,M.D. 1978. Demography and survival under grazing of three Australian semi-arid shrubs. Oikos 30:520-528.

Frasier,G.W., Cox,J.R. and Woolhiser,D.A. 1984. Emergence and seedling survival of two warm-season grasses as influenced by the timing of precipitation: a greenhouse study. Journal of Range management 37:7-11.

Frasier,G.W., Cox,J.R. and Woolhiser,D.A. 1985. Emergence and survival responses of seven grasses for six wet-dry sequences. Journal of Range Management 38:372-377.

Jordaan,P.W. and Nobel,P.S. 1982. Height distributions of two species of cacti in relation to rainfall, seedling establishment and growth. Botanical Gazette 143:511-517.

Joubert,J.G.V. and Van Breda,P.A.B. 1976. Methods of establishing Osteospermum sinuatum in Little Karoo veld. Handboek Weidingsvereniging Suid-Afrika 11:123-124.

Jürgens,N. 1986. Contributions to the ecology of southern African succulent plants. Mitteilungen aus dem Institut für Allgemeine Botanik Hamburg 21:139-365.

Lovegrove,B.G. and Siegfried,W.R. 1986. The distribution and formation of mima-like earth mounds in the western Cape region of South Africa. South African Journal of Science 82:432-436.

Milton,S.J. 1990. Above-ground biomass and plant cover in a succulent shrubland in the southern Karoo, South Africa. South African Journal of Botany 56:587-589.

Milton,S.J. and Dean,W.R.J. 1990. Seed production in rangelands of the southern Karoo. South African Journal of Science 86:231-233.

Milton,S.J., Dean,W.R.J. and Kerley,G.I.H. 1992. Tierberg Karoo Research Centre: history, physical environment, flora and fauna. Transactions of the Royal Society of Southern Africa 48:15-46.

Pyke,D.A. and Thompson,J.N. 1986. Statistical analysis of survival and removal rate experiments. Ecology 67:240-245.

Rutherford,M.C. and Westfall,R.H. 1986. Biomes of southern Africa - an objective categorization. Memoirs of the Botanical Survey of Southern Africa, no. 54. Government Printer, Pretoria. 98pp.

Sala,O.E. and Lauenroth,W.K. 1982. Small rainfall events: an ecological role in semi-arid regions. Oecologia 53:301-304.

Siegel,S. 1956. Non-parametric statistics for the behavioral sciences. McGraw-Hill, Auckland, New Zealand. pp 127-136.

Slatyer,R.O. 1967. Plant-water relationships. Academic press, London. pp 75-77.

Soriano,A and Sala,O.E. 1986. Emergence and survival of Bromus setifolius seedlings in different microsites of a Patagonian arid steppe. Israel Journal

of Botany 35:91-100.

Steenbergh,W.F. and Lowe,C.H. 1969. Critical factors during the first years of life of the Saguaro (Cereus giganteus) at Saguaro National Monument, Arizona. Ecology 50:826-834.

Turner,R.M., Alcorn,S.M., Olin,G. and Booth,J.A. 1966. The influence of shade, soil and water on saguaro seedling establishment. Botanical Gazette 127:95-102.

Turner,R.M., Alcorn,S.M. and Olin,G. 1969. Mortality of transplanted saguaro seedlings. Ecology 50:835-844.

Vidiella,P.E. and Armesto,J.J. 1989. Emergence of ephemeral plant species from soil samples of the Chilean coastal desert in response to experimental irrigation. Revista Chilena de Historia Natural 62:99-107.

Von Willert,D.J., Brinckmann,E., Scheither,B and Eller,B.M. 1985. Availability of water controls Crassulacean acid metabolism in succulents of the Richtersveld (Namib desert, South Africa). Planta 164:44-55.

Werger,M.J.A. 1986. The Karoo and southern Kalahari. In: Hot deserts and arid shrublands, Vol B., eds. M. Evenari, I. Noy-Meyer and D.W Goodall. Elsevier, Amsterdam. pp 283-359.

Westoby,M. 1980. Elements of a theory of vegetation dynamics in arid rangelands. Israel Journal of Botany 28:169-194.

Yeaton,R.I and Esler,K.J. 1990. The dynamics of a succulent karoo vegetation: a study of species association and recruitment. Vegetatio 88:103-113.

Zar,J.H. 1984. Biostatistical Analysis. Prentice-Hall, New Jersey. 718pp.

Zucchini,W. and Adamson,P. 1984. The occurrence and severity of droughts in South Africa. Water Research Commission Report No. 91/1/84, Department of Civil Engineering, University of Stellenbosch. 191pp.

CHAPTER 8

GENERAL CONCLUSIONS

This chapter highlights the major contributions of the thesis as well as the limitations. Where questions have remained unanswered, suggestions for future research are proposed. The objectives of the thesis were:

1. To fill a gap in terms of the knowledge of the reproductive biology of karoo plants,
2. To focus on the reproductive biology of key species in the cyclic succession in order to understand the demographic processes underlying these successional patterns, and
3. To focus on the Mesembryanthema (family Aizoaceae) since the ecology of this group is poorly understood.

The major findings are discussed in relation to these objectives.

8.1 THE REPRODUCTIVE BIOLOGY OF KAROO PLANTS

In arid environments in general, very little is known about population dynamics and population processes, such as dispersal, establishment and dormancy, that depend on the distribution and behaviour of seeds (Kemp 1989). One of the primary contributions of the thesis is that it is the first comprehensive study of seed and seedling biology in the southern Karoo. A feature of the study was that it focussed on spatial as well as temporal heterogeneity; aspects of the research were conducted over a two to three year period. Special emphasis was placed on the role of the microhabitat in influencing vegetation processes. Generalised linear models (GLIM) were used to analyse the seed bank data (McCullagh and Nelder 1983). Although the technique has been available for at least fifteen years, GLIM has not been widely used in the seed bank literature. This thesis highlights the uses of the technique for interpreting seed bank data, which has traditionally been problematic to analyze.

The reproductive behaviour of the species on the study site could largely be explained in terms of the habitats in which they occurred. This was, in turn, related to successional processes on the study site. Species occurring early on in the successional sequence tended to have larger canopy and/or soil seed banks and

dormant seeds. On the other hand, later-successional species had transient seed banks and did not have canopy stored seeds. Because the study was approached largely from an ecological perspective, the physiological controls of seed dormancy and germination were not studied. This is a major gap in the thesis.

The thesis highlights the role of the microhabitat in influencing seedling distributions and thus adult plant distributions. Seeds and seedlings were not distributed randomly in the study site. There were definite patterns in seed and seedling distributions and this appeared to be associated mainly with seed dispersal, since seedling mortality did not differ in different microhabitats. Although the study of spatial and temporal patterns of seed and seedling distributions provided some interesting insights into processes underlying vegetation dynamics, it did not provide an answer to the question, "What limits seedling recruitment in this environment?". An experimental approach is needed to understand the factors which limit seedling recruitment. For example, it is important to establish whether recruitment is seed-limited (Crawley 1990). If seed numbers are not limiting, herbivory and/or granivory may not have such an important impact on long-term plant population stability. In the Karoo, where domestic livestock are the key herbivores, this is a question which requires an urgent answer (Hoffman and Cowling 1897) - numbers of domestic livestock can be readily manipulated for management, which is not the case with locusts and other invertebrate and vertebrate herbivores, (McKenzie and Longridge 1988). One way of approaching this question would be to set up a factorial experiment in which extra seeds are sown into the vegetation in some areas, and not in others (control). By monitoring recruitment, one could establish whether microhabitat availability or competition with adult plants is more important than seed availability in limiting recruitment. Such experiments would have to be long-term because environmental variation may result in some microhabitats being limiting in some years, but not in others. For example, in very dry, hot years, sheltered microhabitats may be the only sites in which recruitment can occur, thus, these sites may be limiting in these years.

8.2 VEGETATION DYNAMICS IN THE SOUTHERN SUCCULENT KAROO

The bulk of the research in this thesis relates to a vegetation model proposed by Yeaton and Esler (1990, Appendix 1). This empirical model, based on the interpretation of patterns of species distributions and numbers, describes the dynamics of the study site in terms of a predictable sequence of species replacements, determined primarily by biotic interactions. This model permitted the design of experiments which asked process-type questions. Some of the data in the thesis corroborates the model, but there are still several unanswered questions. Can, for example, the model be generalised to include the entire Succulent Karoo? *Heuweltjies* are an important component of the model which assumes that disturbance within the system, created by *heuweltjies*, drives the species replacements and creates a spatially and temporally dynamic array of habitats which different species exploit. Thus, there is an active process involved in the creation, maturation and final senescence of *heuweltjies*. In other words, *heuweltjies* are dynamic entities in the succulent karoo landscape. There has been much speculation as to the origins of *heuweltjies*, although it now is generally accepted that they are created by termites (Milton and Dean 1990). *Heuweltjies* are considered by some to be very stable features in the landscape (*heuweltjies* in the Clanwilliam district of the Karoo have been dated to ca. 4 000 years old, Moore and Picker 1991). If *heuweltjies* are so stable, then there could be a problem equating time scales involved in vegetation succession with the time scales involved in the turnover of *heuweltjies*. At Tierberg, *heuweltjies* do appear to be at different dynamic stages. Tierberg is a marginal Succulent Karoo site as well as a marginal site with respect to *heuweltjie* distributions. It is easy to imagine that the turnover of *heuweltjies* on this site could be more rapid than in the main areas of their distribution since the creation of termite colonies may be more stochastic than in other areas of the Succulent Karoo.

Several other questions arising from the vegetation dynamics model can be applied to the Succulent Karoo as a whole. If *heuweltjies* are indeed central to the plant

dynamics, does this mean that increased density and/or turnover of *heuweltjies* would permit increased species richness? Perhaps the presence of *heuweltjies* is an underlying determinant of the unparalleled species diversity in the Succulent Karoo (Cowling et al. submit.). It is possible that the presence of *heuweltjies* not only affects beta and gamma diversity (Knight et al. 1989), but alpha diversity too, via disturbance mediated coexistence. At present there is no general study of vegetation associated with *heuweltjies* over their entire range. Certainly, the present feeling is that *heuweltjies* can not be generalised into one group. Future research is required to investigate *heuweltjie* dynamics over their entire range. A long-term monitoring programme would be useful to determine the rates of change in biotic and abiotic elements on *heuweltjies*.

The fact that most species have transient seed banks in the Succulent Karoo may provide another explanation for the high alpha diversity in this area. As mentioned in Chapter 1, the Succulent Karoo is unusual in that short- to medium-lived (ca. 3-10 years) succulent shrubs are common in the vegetation. Occasional, but catastrophic, droughts have been recorded in this region. These have resulted in mortalities of up to 90% for certain species (Von Willert et al. 1985). This thesis has shown that many species in the Succulent Karoo have transient seed banks. Population reduction of some species during drought may allow other species to increase in numbers, depending on what seeds are present in the seed bank. Thus, the high diversity of species in the area may also be a result of differential reproductive output of species, leading to a lottery-mediated coexistence (Cowling et al. submit.).

Although it has been demonstrated that vegetation turnover in this environment is largely a result of the sequence in which various plant species establish, the rate at which these changes occur remains unknown. Westoby et al. (1989) suggested that climatic events largely determine when these vegetation "states" and transitions occur. This thesis contributes significantly to an understanding of the vegetation "states" in the Succulent Karoo, and how they are derived, but a gap still exists with respect to the time scales involved in the vegetation change. It is

essential that more long-term studies on field recruitment are initiated. The use of the rainfall simulation programme GENRAIN (Zucchini and Adamson 1984) has been demonstrated in this thesis. A long-term understanding of when reproductive events occur would allow this programme to be used in a predictive manner for sound farming and conservation practices.

8.3 STUDIES ON MESEMBRYANTHEMA

As was highlighted in the introductory chapter, very little ecological work has been conducted on the Mesembryanthema. This thesis represents one of the first comprehensive attempts at understanding the ecology of this group. One of the major findings is that canopy-stored seed banks in this group are not as common as previously believed (Ihlenfeldt 1971, Hoffman and Cowling 1987), certainly for the study area where this thesis was conducted. However, it is not easy to generalise when one considers that there are over 2 000 recognised species in this group (Hartmann 1991). Another finding of this thesis is that the group plays an important role in the dynamics of the vegetation on the study site. Seedlings of mat-forming Mesembryanthema can colonise open microhabitats since they are tolerant of extreme conditions once established. These species then provide seed-traps and possibly shelter for later successional species in the woody shrub guild, many of which are economically important because of their palatability. This highlights a variety of possibilities for the use of some species of Mesembryanthema in restoration ecology programmes. A large part of the Karoo is severely degraded and requires not only active maintenance of species diversity but also active attempts at radical range improvement (B. Bayer, pers. comm., Worcester Veld Reserve, Worcester). Mat-forming Mesembryanthema could be used as the first step in sequential re-seeding of vegetation. An added advantage of using this group is that their seeds are contained in easily collected capsules. Many attempts have so far been made to improve karoo vegetation by sowing seed directly into the vegetation (Joubert and Van Breda 1976), but these have failed because of insufficient understanding of the dynamics of the vegetation (B. Bayer,

Pers. Comm., Worcester Veld Reserve, Worcester). There is now a strong realisation that by understanding recruitment processes and vegetation dynamics in general, farming and conservation management can be conducted with more success (Danckwerts and Teague 1987).

8.4 REFERENCES

Cowling,R.M., Esler,K.J., Midgely,G.F. and Honig,M.A. Submit. Plant Functional diversity, species diversity and climate in arid and semi-arid southern Africa. Journal of Arid Environments.

Crawley,M.J. 1990. The population biology of plants. Philosophical Transactions of the Royal Society of London 330:125-140.

Danckwerts,J.E and Teague,W.R. 1987. Veld Management in the Eastern Cape. Pasture Research, Stutterheim. 337pp.

Hartmann,H.E.K. 1991. Mesembryanthema. In: Systematics, biology and evolution of some South African taxa, eds. P. Goldblatt, H.E.K. Hartmann, E.G.H. Oliver, H.P. Linder and B.E. van Wyk, Contributions to the Bolus Herbarium 13:75-157.

Hoffman,M.T. and Cowling,R.M. 1987. Plant physiognomy, phenology and demography. In: The Karoo biome: A preliminary synthesis. Part 2. - vegetation and history, eds. R.M. Cowling and P.W. Roux. South African National Scientific Programmes Report No. 142, Council for Scientific and Industrial Research, Pretoria. pp 1-34.

Ihlenfeldt,H.D. 1971. Some aspects of South African biomes. In: Ecological effects of fire in South African ecosystems, eds. V. Booysen and N.M. Tainton. Ecological Studies: Analysis and Synthesis Vol. 48, Springer-Verlag, Berlin. pp 1-17.

Joubert,J.G.V. and Van Breda,P.A.B. 1976. Methods of establishing Osteospermum sinuatum in Little Karoo veld. Handboek Weidingsvereniging Suid-Afrika 11:123-124.

Kemp,P.R. 1989. Seed banks and vegetation processes in deserts. In: Ecology of soil seed banks, eds. M.A. Leck, V.T. Parker and R.L. Simpson, Academic Press, New York. pp 257-281.

Knight,R.S., Rebelo,A.G., Siegfried,W.R. 1989. Plant assemblages on mima-like earthmounds in the Clanwilliam District, South Africa. South African Journal of Botany 55:465-472.

McCullagh,P. and Nelder,J.A. 1983. Generalised linear models. Chapman and Hall, London. 261pp.

McKenzie,B. and Longridge,M. 1988. Proceedings of the locust symposium. South African Institute of Ecologists Bulletin, special issue. 159pp.

Milton,S.J. and Dean,W.R.J. 1990. Mima-like mounds in the southern and western Cape: are the origins so mysterious? South African Journal of Science 86:231-233.

Moore,J.M. and Picker,M.D. 1991. *Heuweltjies* (earth mounds) in the Clanwilliam district, Cape Province, South Africa: 4 000-year-old termite nests. Oecologia 86:424-432.

Von Willert,D.J., Brinckmann,E., Eller,B.M. and Scheitler,B. 1983. CO_2 exchange of CAM exhibiting succulents in the southern Namib desert in relation to microclimate and water stress. Photosynthesi Research 4:289-298.

Westoby,M., Walker,B. and Noy-Meir,I. 1989. Opportunistic management for rangelands not at equilibrium. Journal of Range Management 42:266-274.

Yeaton,R.I. and Esler,K.J. 1990. The dynamics of a succulent karoo vegetation: a study of species association and recruitment. Vegetatio 88:103-113.

Zucchini,W. and Adamson,P. 1984. The occurrence and severity of droughts in South Africa. Water Research Commission report No. 91/1/84, Department of Civil Engineering, University of Stellenbosch. 191pp.

APPENDIX 1

THE DYNAMICS OF A SUCCULENT KAROO VEGETATION: A STUDY OF SPECIES ASSOCIATION AND RECRUITMENT

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The dynamics of a succulent karoo vegetation

A study of species association and recruitment

R. I. Yeaton [1] & K. J. Esler [2]

[1] *Department of Botany and UN-FRD Research Unit for Plant Growth and Development, University of Natal, Pietermaritzburg 3200*; [2] *Department of Botany, University of Cape Town, Rondebosch 7700, South Africa*

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Abstract

Strong inference techniques were used in a preliminary study of the structure and dynamics of the vegetation in the Prince Albert region of the Great Karoo, South Africa. Seedling emergence studies indicate that open areas in the interstices of the existent vegetation are colonized by mound-building species of the Mesembryanthemaceae. Later, these species serve as sites of establishment for seedlings of several species of woody shrubs. Eventually, the woody shrubs replace the mound-building mesems through interspecific competition. The woody shrubs persist in the community until they reach senescence and die or are removed through overgrazing. Superimposed on this dynamic pattern is a further temporal pattern involving a combination of disturbance and subsequent soil changes. Much of this effect is caused by fossorial animals, which are associated with large circular (10–20 m diameter) mounds. Burrowing by these animals changes the soil characteristics and establishes an additional sequence of vegetation succession in which the mounds serve as refuges from which non-palatable species, such as *Pteronia pallens*, can invade the rangeland. Later, as the mounds are abandoned and disturbance effects cease, more palatable species, such as *P. empetrifolia*, will replace *P. pallens*, overcoming finally the effects of the adjacent mounds on the surrounding vegetation.

Nomenclature: follows Gibbs Russell, G. E., Welman, W. G., Retief, E., Immelman, K. L., Germishuizen, G., Pienaar, B. J., Van Wyk, M. & Nicholas, A. 1987. List of species of southern African plants. Mem. Bot. Surv. S. Afr. 56: 1–270.

Introduction

The Karoo comprises an extensive arid and semi-arid rangeland occupying roughly one third of South Africa. Over the last three centuries the diverse flora of this region has undergone wide-scale and dramatic change (Acocks 1975; Roux & Vorster 1983). These changes, attributed primarily to over-exploitation coupled with a variable and unpredictable climate, have resulted in the replacement of the grass component of these rangelands by unpalatable weedy species of the

Mesembryanthemaceae and woody shrubs. Research in community ecology in the Karoo is notably lacking despite its importance in developing an underlying understanding of the mechanisms which drive the system and lead to replacement of mesic types of vegetation by more arid forms (Cowling 1986; Bond 1987). There are two main reasons for the lack of quantitative representation of the dynamics of Karoo plant communities. First, the detection of changes in the shrub assemblages is difficult due to the very slow rate of population turnover. Second, for southern African ecologists, the continuing debate on the role of competition in determining community structure has led to the belief that predictable series of species replacements are not possible in a system whose dynamics are governed by spatially and temporally variable climatic sequences (Hoffman & Cowling 1987). However, it is becoming increasingly evident from the literature on the structure and dynamics of arid and semiarid zones that predictable patterns in species interactions and community structure are the rule in such environments (Yeaton 1978; Yeaton & Cody 1979; Vasek 1979; Vandermeer 1980; Fonteyn & Mahall 1981; Phillips & MacMahon 1981; Cody 1986; McAuliffe 1988; Yeaton 1988). In this study, we show that the patterns of relative abundance and distribution among and within Karoo plant species and the temporal and spatial patterns of their recruitment provide an adequate and predictable description of the dynamics of these systems.

Study area

The study area is located at 725 m elevation on the farm, Tierberg, which is roughly 25 km east of Prince Albert, Cape Province, South Africa (33° 9′ S, 22° 16′ E). Temperatures at the nearest longterm recording station, Beaufort West (32° 19′ S, 22° 38′ E, elevation 868 m) averaged over the 1936–1950 period were for annual maximum, 25.3 °C, and for annual minimum 10.6 °C (Weather Bureau 1954). The highest monthly average temperature recorded during this period was 32.5 °C in January and the lowest monthly average temperature was 4.9 °C in July (Weather Bureau 1954). Average annual relative humidity during this period was 63%. Rainfall in this area averages between 100 and 300 mm per year with a 60–65% reliability (Venter, Mocke & De Jager 1986). The peak rainfall months are March and September and the resultant vegetation is succulent Karoo (Acocks 1975; Rutherford & Westfall 1986). Soils in the area are sandy and weakly structured and are derived from the Karoo sediments of the Ecca series (Ellis & Lambrechts 1986; Visser 1986).

The gently undulating topography of the site, dissected by drainage lines, supports a homogeneous set of plant species. Interspersed regularly throughout the study site are Mima-like earth mounds (Cox 1984), known locally as 'heuweltjies', which support a generally different and less homogeneous set of plant species. Our study concentrates on the plant association found off the 'heuweltjies' characterized by either of two closely related Asteraceous shrubs, *Pteronia pallens* or *P. empetrifolia*. These two species appear to occupy distinctly different habitats within the study site. *Pteronia pallens* is found more commonly along drainage lines and on 'heuweltjies', while *P. empetrifolia* occurs more often on the gentle slopes and upper flats of the shallow rises between the drainage lines. The latter habitat, however, is often used by *P. pallens* and extensive overlaps of the two species occur. The other members of this plant association are *Brownanthus ciliatus*, *Drosanthemum montaguense*, *Eberlanzia* c.f. *vulnerans*, *Galenia fruiticosa*, *Hereroa latipetala*, *Osteospermum sinuatum*, *Rhinephyllum* c.f. *graniforme*, *R. macradenium*, *Ruschia approximata* and *Tetragonia spicata*.

The study area had been previously grazed by sheep until 1986 when they were excluded by fencing. After this date only hares (*Lepus capensis*) and antelope (*Raphicerus campestris*, *Sylvicapra grimmea* and *Tragelaphus strepsiceros*) had access to the area for browsing.

Methods

Fifty 5 m × 5 m quadrats were sampled over an approximately 0.3 km^2 area in the following pattern. A series of five quadrats characterized by *Pteronia empetrifolia* and a further five quadrats dominated by *P. pallens* were sampled on gradual (0–0.5°) slopes near the tops of each of five rises. Care was taken to avoid drainage lines where moisture concentrates seasonally. Increased soil moisture results in larger individuals of the species occurring both in the drainage lines and in the upland sites as well as the addition of other species found only in the drainage lines. The identity of each individual taller than 10 cm was recorded and its length along the long axis (L) and its greatest width at right angles to the length (W) measured. Cover of each individual was calculated according to the formula π LW/4. The average number of individuals and their average cover were determined for each quadrat and the mean and standard error of these averages calculated for each set of twenty-five quadrats characterized by *P. empetrifolia* and *P. pallens*. From these data the relative abundances and covers of each species were calculated for each set of quadrats. Species with relative abundances or covers less than 1% were considered too rare to have a major impact on community dynamics and were excluded from the analysis. The relative abundances and covers on *P. empetrifolia* and *P. pallens* quadrats were then recalculated for the species remaining. Next we distinguished two guilds from the total species lists based on their growth forms; one composed of taller woody shrubs (woody shrub guild), and the other composed of the remainder of the species and generally more decumbent in growth form. The latter guild is made up entirely of members of the Mesembryanthemaceae (mesem guild).

We next examined the pattern of differences between the two guilds comprising the plant association found on quadrats characterized by the two *Pteronia* species. We summed the mean relative abundance of each species with its mean per cent cover for *P. empetrifolia* and for *P. pallens* quadrats and used a Sign test to compare the differences between the two sets of quadrats (Siegel 1956).

The locations of seedlings of each species were recorded for seven microhabitats, which we recognized in the convex upland areas where the study was conducted. (Seedlings are either individuals established during the previous year or young individuals shorter than 10 cm, smaller than 2 cm in diameter and with unlignified and unbranched main stems, which established in the last few years). These microsites are:

1) open; seedlings established on fine sands and clays between the mounds occupied by larger members of the plant association.
2) large rocks; seedlings established adjacent to or under the edge of rocks where fine sands and organic debris have collected.
3) sheet wash; seedlings established in areas where plant debris, moved by surface flow of water, has been trapped between mounds.
4) base of plant; seedlings established on the coarser sands and leaf litter found on mounds at the base of woody shrubs.
5) side of mound; seedlings established, usually in partial shade on the compacted fine sands of the runoff slopes on the edges of the mounds.
6) in a mound-building Mesembryanthemaceae; seedlings established in organic-rich sands within or under the edge of the plant's canopy.
7) in a dead mound-building Mesembryanthemaceae; seedlings established in organic-rich sands under the canopy of a dead plant.

These microhabitats tended to represent two broad categories of 'safe sites' for seedlings. The 'open' microsite is in areas not shaded by plants where the organic debris in the soil is insufficient to hold moisture for any significant length of time. Seedlings establishing in this microhabitat are more likely to be seasonally moisture-stressed than seedlings establishing in the other six recognized microhabitats. These microhabitats form a second category of 'safe sites', which are wetter than the 'open' microhabitats because they are either shaded to some extent or have sufficient organic material in the soil to retain moisture longer into the dry season. We compared the dis-

tribution of the seedlings of the woody shrub guild with that of the mesem guild in these two categories of 'safe sites' by a Chi-square for a 2 × 2 contingency table (Siegel 1956).

Association of species was tested using regression analyses of average numbers and covers for pairs of species found on the fifty quadrats sampled (Grieg-Smith 1983).

Next we examined what appeared to us to be critical points in the above regression analyses of association. As many of the negative associations involved *P. pallens* with members of the woody shrub guild and the positive associations of the same members of this guild with *P. empetrifolia*, we looked at the relationship between the two *Pteronia* species. We used nearest-neighbour analysis to determine if intraspecific and interspecific interactions were occurring (Pielou 1960). Individuals of *P. empetrifolia* and *P. pallens* were chosen randomly by walking 1 m-wide line transects. The length and width of each *Pteronia* individual along the line transect was measured and its identity recorded. Then the length and width of the nearest-neighbour *Pteronia* and the distance from plant centre to plant centre were measured and the identity of the nearest-neighbour *Pteronia* recorded. Such measurements were made following the operational definitions of Yeaton & Cody (1976) until at least 100 nearest-neighbour pairs were obtained for each intraspecific and interspecific cases. Based on these operational definitions, these measurements were taken only in homogeneous and continuous vegetation for pairs of individuals not occurring in or separated by drainage lines and away from 'heuweltjies'. Furthermore these measurements are made only if no individual of another species is growing such that its canopy intersects a straight line between the intra- or interspecific pair of individuals measured. The distance between the centers of the two nearest-neighbours was regressed against the sum of the covers of the two individuals for each intraspecific and interspecific data set. A positive relationship between these parameters indicates that a competitive interaction is occurring such that the distance apart that two individuals establish limits the sizes to which they can grow.

Next, because we observed several instances in which *P. empetrifolia* is growing beneath *P. pallens* and *P. pallens* appeared to be the worst for it, we contrasted the vigour of the latter individuals with the nearest *P. pallens* growing without *P. empetrifolia* beneath it. A 0.2 m × 0.2 m piece of clear plastic, marked off in twenty-five 40 mm × 40 mm squares was placed on top of the centre of each *P. pallens* and the number of squares with green foliage within a depth of 0.1 m into the canopy counted. Data, obtained from a sample of thirty adjacent *P. pallens* with *P. empetrifolia* growing beneath them and thirty adjacent *P. pallens* growing alone, were compared statistically with a Median test (Siegel 1956).

Second, we measured the effect of the woody shrub guild on the decumbent mesem guild. Several members of the woody shrub guild (notably *P. empetrifolia* and *Drosanthemum* at the 0.01 level but also *Osteospermum* and *Tetragonia* at the 0.05 level) were negatively associated with *Eberlanzia*, the most abundant member of the decumbent mesem guild. However, because their seedlings commonly establish in this species, we measured the effect of these woody shrubs on the latter. We repeated these measurements for *Brownanthus*, the species of Mesembryanthemaceae most similar in size and growth form to *Eberlanzia*, and also observed to have seedlings of the woody shrub guild establishing next to or within its canopy. In each case the cover of the woody shrub, the cover of the decumbent, mound-building Mesembryanthemaceae and its vigour were measured. Vigour was measured as described above in the volume of the canopy immediately next to the woody shrub. Vigour of each individual was compared with the cover of the woody shrub growing through its canopy by a Spearman Rank Correlation test (Siegel 1956) for these two mound-building species. In addition, vigour was compared with the cover of each of the two species using the same statistical procedure.

We also quantified the position of establishment of at least one hundred seedlings of the woody shrub guild as being either within the canopy or at the edge of the canopy of these two mound-building species and tested for differences

between these two species by a Chi-square test for 2 × 2 contingency tables (Siegel 1956).

Third, as these two decumbent, mound-building species are negatively associated with one another, we examined their potential interactions on mounds occupied by both species. We recorded which species was overgrowing the other and the conditions of the stems of the two species where their canopies overlapped. We assume that if no interaction occurs between these two species there will be equal numbers of *Eberlanzia* overtopping live and dead *Brownanthus* and vice-versa. A Chi-square one-sample test was used to test this assumption (Siegel 1956). A similar procedure was used to study the interactions of a third mound-building species, *Rhinephyllum macradenium*, which is also negatively associated with *Eberlanzia*.

Results

A total of twelve plant species were represented by a minimum of 1% occurrence in their relative abundance or their per cent cover on quadrats characterized either by *Pteronia empetrifolia* or *P. pallens* (Table 1). Differences are present between quadrats characterized by *P. empetrifolia* and *P. pallens*. *Galenia* dominates *P. empetrifolia* quadrats in terms of both relative numbers and per cent cover while *Eberlanzia* and *P. pallens* dominate *P. pallens* quadrats in relative numbers and per cent cover respectively. In general, there are higher relative numbers and relative covers for species included in the woody shrub guild on *P. empetrifolia* quadrats than on *P. pallens* quadrats while the opposite happens for members of the mesem guild; higher relative numbers and relative covers occur on *P. pallens* quadrats ($P = 0.04$).

A total of 866 seedlings were located on the study area and their microhabitat utilization quantified (Table 2). Differences exist between the seedlings of members of the two guilds in their successful establishment in microhabitats (Table 3, $P \ll 0.001$). Ninety-three per cent of the seedlings of members of the woody shrub guild and 35% of the seedlings of members of the mesem guild established in the wetter microhabitats. In contrast, only 7% of the seedlings of the woody shrub guild established successfully in the drier open microhabitats while 65% of the seedlings of the mesem guild established in the open.

Regression analyses of the association of species for their total number of individuals or their total cover on the fifty quadrats sampled yields several significant positive and negative pairwise associations (Table 4). As expected, a strong negative association happens between *P. empetrifolia* and *P. pallens* as an artifact of the sampling process. More important relationships transpire when comparing the associations of other species with the two *Pteronia* species. All other members of the woody shrub guild are positively associated with *P. empetrifolia* and negatively associated with *P. pallens*. Furthermore, there are associations among various combinations of the woody shrub guild at the 0.01 level (Table 4). In contrast, only one positive results between members of the mesem guild, *Eberlanzia* with *Rhinephyllum graniforme*. When *P. pallens* is removed from consideration, many of the remaining negative associations involve *Eberlanzia* and other members of the mesem guild (Table 4). Except for its interaction with *P. empetrifolia*, *Eberlanzia* has negative associations only with other species of Mesembryanthemaceae including *Drosanthemum*, a member of the woody shrub guild.

There are significant linear and positive, non-zero relationships between distance (X) and the sum of plant covers (Y) for all intra- and interspecific nearest-neighbour pairs of *P. empetrifolia* and *P. pallens* (for *P. empetrifolia* against itself; $Y = 0.35X + 40.33$, $r = 0.681$; for *P. pallens* against itself, $Y = 0.69X + 35.09$, $r = 0.832$; for *P. empetrifolia* against *P. pallens*, $Y = 0.29X + 62.21$, $r = 0.520$; P for all cases < 0.01). The average vigour of *P. pallens* growing alone is 87% and 49% when *P. empetrifolia* has established beneath it. When *P. empetrifolia* has established under the canopy of *P. pallens*, the vigour of the latter is significantly reduced when com-

Table 1. The density, relative abundance, cover and relative cover of species with greater than than 1% relative abundance or cover on quadrats characterized by either *Pteronia empetrifolia* or *P. pallens* in the Great Karoo at the farm Tierberg, Cape Province, South Africa. Mean values (+ SE) are given per 25 m^2 quadrat.

Pteronia empetrifolia quadrats				*Pteronia pallens* quadrats			
Species	$\bar{X}$	S.E.	Relative abundance (%)	Species	$\bar{X}$	S.E.	Relative abundance (%)
Number of individuals				Number of individuals			
Pteronia empetrifolia	6.04	0.16	5.4	*Pteronia empetrifolia*	0.24	0.18	0.2
P. pallens	0.84	0.26	0.7	*P. pallens*	8.60	0.23	8.8
Osteospermum sinuatum	13.88	0.36	12.3	*Osteospermum sinuatum*	6.20	0.25	6.3
Galenia fruiticosa	31.64	0.42	28.1	*Galenia fruiticosa*	15.88	0.42	16.2
Tetragonia spicata	4.88	0.28	4.3	*Tetragonia spicata*	1.24	0.25	1.3
Drosanthemum montaguense	11.60	0.42	10.3	*Drosanthemum montaguense*	2.76	0.57	2.8
Ruschia approximata	5.72	0.56	5.1	*Ruschia approximata*	6.64	0.59	6.8
Rhinephyllum graniforme	0.56	0.39	0.6	*Rhinephyllum graniforme*	2.36	2.18	2.4
R. macradenium	12.56	0.67	11.2	*R. macradenium*	9.20	0.83	9.4
Brownanthus ciliatus	4.20	0.50	3.7	*Brownanthus ciliatus*	7.48	0.53	7.6
Hereroa latipetala	5.96	0.64	5.3	*Hereroa latipetala*	11.44	0.57	11.7
Eberlanzia c.f. *vulnerans*	14.68	0.83	13.0	*Eberlanzia* c.f. *vulnerans*	25.92	0.75	26.5
Cover	$\bar{X}$	S.E.	% Cover	Cover	$\bar{X}$	S.E.	% Cover
Pteronia empetrifolia	6204	17	11,7	*Pteronia empetrifolia*	157	6	0.3
P. pallens	1076	12	2.0	*P. pallens*	17961	275	32.0
Osteospermum sinuatum	6931	9	13.1	*Osteospermum sinuatum*	2757	7	4.9
Galenia fruiticosa	13403	8	25,3	*Galenia fruiticosa*	6802	10	12.1
Tetragonia spicata	532	3	1.0	*Tetragonia spicata*	117	3	0.2
Drosanthemum montaguense	8846	12	16.7	*Drosanthemum montaguense*	2333	17	4.2
Ruschia approximata	1287	8	2.4	*Ruschia approximata*	1728	10	3.1
Rhinephyllum graniforme	107	6	0.2	*Rhinephyllum graniforme*	468	9	0.8
R. macradenium	3856	12	7.3	*R. macradenium*	3453	16	6.1
Brownanthus ciliatus	1868	13	3.5	*Brownanthus ciliatus*	3691	11	6.6
Hereroa latipetala	1230	9	2.3	*Hereroa latipetala*	2252	9	4.0
Eberlanzia c.f. *vulnerans*	7707	18	14.5	*Eberlanzia* c.f. *vulnerans*	14464	16	25.7

pared with *P. pallens* growing alone (Table 5, $P < 0.001$).

The vigour of the two common mound-building species, *Eberlanzia* and *Brownanthus*, is strongly affected by the size of the members of the woody shrub guild which establish under or next to its canopy. For both species, vigour is negatively correlated with the cover of the member of the woody shrub guild (for *Eberlanzia*, n = 110, Spearman's r = 0.80; for *Brownanthus*, n = 104, Spearman's r = 0.52; $P \ll 0.01$ for both cases). No significant relationship arises between the vigour of *Brownanthus* and its cover while the cover of *Eberlanzia* correlates with its vigour; larger individuals had reduced vigour (Spearman's r = 0.46, $P < 0.01$). Seedlings of the woody shrub guild establish more frequently at the edge of the canopy of *Brownanthus* and rarely under its canopy while the reverse is true for *Eberlanzia* (Table 6, $P < 0.001$).

Eberlanzia appears to be replacing *Brownanthus* over time when large individuals of each species are in contact with one another on a mound (Table 7). In most cases, dead stems of *Brown-*

Table 2. Microhabitat utilization by seedlings of species found on covex upland sites at the farm, Tierberg, in the Great Karoo, Cape Province, South Africa. Pe = *Pteronia empetrifolia*, Pp = *P. pallens*, Os = *Osteospermum sinuatum*, Gf = *Galenia fruiticosa*, Ts = *Tetragonia spicata*, Dm = *Drosanthemum montaguense*, Ra = *Ruschia approximata*, Rg = *Rhinephyllum graniforme*, Rm = *R. macradenium*, Bc = *Brownanthus ciliatus*, Hl = *Hereroa latipetala*, Ev = *Eberlanzia* c.f. *vulnerans*.

	Microhabitat						
Species	Open	Rock	Sheet wash	Plant base	Mound side	Live mesem	Dead mesem
Pe	3	5	26	35	18	21	1
Pp	4	20	43	24	62	61	59
Os	1	0	1	1	1	53	5
Gf	28	4	5	4	26	3	0
Ts	2	2	2	5	2	22	4
Dm	4	2	1	1	0	8	2
Ra	9	1	1	0	3	0	0
Rg	20	1	10	1	13	0	0
Rm	32	2	3	0	3	0	0
Bc	13	0	1	0	0	0	0
Hl	71	1	2	11	15	2	1
Ev	48	4	4	6	13	4	0

Table 3. The distribution of seedlings of the woody shrub guild and Mesembryanthemaceae guild with respect to open and sheltered microhabitats at the farm, Tierberg, Cape Province, South Africa.

	Open sites	All other sites
Woody shrub guild	42	529
Mesembryanthemaceae guild	193	102

anthus occur underneath the vigorous canopy of *Eberlanzia* ($P < 0.005$). In addition, the only situations in which seedlings of one species established under the canopy of the second, were those of *Eberlanzia* under large individuals of *Brownanthus* (Table 7). A similar situation exists for the interaction of *R. macradenium* with *Eberlanzia*, only in this case the outcome reverses with *R. macradenium* being the winner (Table 8, $P < 0.005$).

Discussion

In order to understand the dynamics of this plant community we considered the differences between the quadrats characterized by *Pteronia empetrifolia* and *P. pallens* and the inferred pattern of replacement of species as a result of interspecific competition within and between guilds. The species which seems to be key to this system is *Eberlanzia* c.f. *vulnerans*. It is the most abundant member of the mesem guild on both *P. empetrifolia* and *P. pallens* quadrats. It is less common on *P. empetrifolia* quadrats where members of the woody shrub guild establish under its canopy. *Eberlanzia* is a multiple-stemmed, spinescent shrub which builds mounds by the capture of wind- and water-transported sands and organic materials at its base. The stems and branches of its canopy are sparsely packed so that light levels are high on the soil surface beneath it. Such a species provides an ideal refuge for palatable woody shrubs such as *P. empetrifolia*, *Osteospermum* and *Tetragonia*. Seedlings of these species are frequently found established within the canopy of *Eberlanzia* but as they grow larger,

Table 4. The level of association of species pairs for members of the plant association found on convex, upland slopes at the farm, Tierberg, Cape Province, South Africa. The letter in parentheses refer to whether the significant relationship occurred for numbers of individuals (N) or cover (C). Abbreviations for species names are the same as given in Table 2.

Level of association	Association	
	Positive	Negative
($P < 0.001$)	Pe/Os (C) Pe/Gf (N) Pe/Ts (N) Pe/Dm (N)	Pp/Os (N,C) Pp/Gf (N,C) Pp/Ts (N,C) Pp/Dm (N,C) Bc/Ev (N) Rm/Ev (N)
($P < 0.01$)	Os/Ts (N) Os/Dm (N) Gf/Dm (N) Rg/Ev (C)	Rm/Hl (N) Pe/Ev (N) Dm/Ev (C)
($P < 0.05$)	Pe/Os (N) Pp/Bc (N) Pp/Rg (N,C) Pp/Ra (C) Pp/Hl (C) Dm/Gf (C) Os/Gf (N) Bc/Rm (N,C) Ra/Rm (C) Ev/Hl (N) Ev/Rg (N)	Pe/Hl (N) Os/Ra (N) Bc/Gf (N) Bc/Os (C) Bc/Ev (C) Bc/Hl (N) Dm/Ev (C) Dm/Rg (N,C) Ra/Hl (C) Rm/Ev (C)

Table 5. The effects of *Pteronia empetrifolia* growing under canopies of *P. pallens* on their vigour.

	Vigour	
	< Median	> Median
Pteronia pallens with *P. empetrifolia*	26	4
Pteronia pallens without *P. empetrifolia*	4	26

kill off its centre. These species would eventually dominate the mound, completely replacing *Eberlanzia*, were it not for the grazing pressure applied by sheep and other browsers.

Table 6. The establishment position of seedlings with respect to the canopies of the two mound-building species of Mesembryanthemaceae, *Eberlanzia* c.f. *vulnerans* and *Brownanthus ciliatus*.

Species	Canopy	
	Edge	Under
Eberlanzia c.f. *vulnerans*	12	43
Brownanthus ciliatus	41	14

Table 7. The replacement of *Brownanthus ciliatus* by *Eberlanzia* c.f. *vulnerans* on mounds formed by the former species at the farm, Tierberg, Cape Province, South Africa.

	Number of occurrences
Adults	
Eberlanzia with dead *Brownanthus*	78
Brownanthus in dead *Eberlanzia*	7
Both *Eberlanzia* and *Brownanthus* alive	15
Seedlings	
Eberlanzia in a dead adult *Brownanthus*	9
Eberlanzia in a live adult *Brownanthus*	15
Brownanthus in a dead adult *Eberlanzia*	0
Brownanthus in a live adult *Eberlanzia*	0

Table 8. The replacement of *Eberlanzia* c.f. *vulnerans* by *Rhinaphyllum macradenium* on mounds formed by the former species at the farm, Tierberg, Cape Province, South Africa.

Adults	Number of occurrences
Rhinephyllum with dead *Eberlanzia*	22
Eberlanzia with dead *Rhinephyllum*	6
Both *Rhinephyllum* and *Eberlanzia* alive	2
Both *Rhinephyllum* and *Enberlanzia* dead	7

The next two most abundant members of the mesem guild in cover are *Brownanthus* and *Rhinephyllum macradenium*. *Brownanthus* is frequently found at the edge of 'heuweltjies' or slightly downslope from them. It also is multiple-stemmed and soil and organic debris accumulate at its base. However, it may be less suitable as a

site of establishment for members of the woody shrub guild because its canopy is more dense and it lacks spinescence. As the central portions of *Brownanthus* die from senescence, this species serves as a site of establishment for *P. pallens*, a species rarely utilized by browsers. Mounds built by *Brownanthus* are frequently colonized by *Eberlanzia*, individuals of which replace the former over time. *Rhinephyllum macradenium* also occupies mounds but it does not appear that its multiple-lobed, decumbent growth form is responsible for the development of the mound. *Rhinephyllum macradenium* is rarely found on mounds with *Eberlanzia* (37 instances recorded in a 4 hr search) but when they do occur together, *Eberlanzia* appears to be the worst off. The other members of the mesem guild either occupy mounds at the base of members of the woody shrub guild (*Ruschia approximata*) or stand as individuals on the open flats (*Hereroa latipetala*, *Rhinephyllum graniforme*). The latter three species and *Rhinephyllum macradenium* rarely serve as sites of establishment for seedlings of the woody shrub guild. Thus, *Eberlanzia* serves as the site of establishment for most palatable members of the woody shrub guild while the dying centre of *Brownanthus* acts as the site of establishment for the unpalatable woody shrub, *P. pallens*. Within the mesem guild three species appear to be replacing one another over time. *Brownanthus*, found adjacent to or downslope from 'heuweltjies', is replaced by *Eberlanzia* which is later ousted by *R. macradenium*. It seems logical to conclude that as *Brownanthus* is first in this successional sequence and that as *P. pallens* frequently establishes within its dying centre. *P. pallens* is an earlier successional species in this vegetation than *P. empetrifolia*. We have shown that when the two species occur together they compete. *Pteronia empetrifolia* reduces the vigor of *P. pallens*. As it is rare to find a seedling of *P. pallens* established under a large *P. empetrifolia*, *P. empetrifolia* must replace *P. pallens* successionally. This pattern is not simply the result of differential browsing of the palatable and unpalatable species of *Pteronia* within the dead centers of *Brownanthus* as seedlings of *P. empetrifolia* establish frequently in other unprotected microhabitats within the study area (sheet wash).

What then is the nature of the disturbance that initiates the sequence of species replacement within this Karoo plant community? The death of a palatable woody shrub species would expose the soil mound to wind and rain and subsequent erosion. The open area is colonized by a member of the mesem guild which may build a new mound and initiate the successional sequence again. Similar sequences have been previously documented for plant associations in other arid and semi-arid regions (Yeaton 1978; Vasek & Lund 1980; Yeaton 1990). But what determines whether the successful mound-builder is *Brownanthus* or *Eberlanzia*? And what factors determine the species of *Pteronia* which establish within their canopies? Without answers to these questions patterns of species replacements would be unpredictable. Thus the factors which initiate the establishment of one species preferentially over another are the ones critical to our developing a predictive understanding of the pattern of dynamics within this community.

The major factor determining which species will establish first may be soil changes arising from the presence of the adjacent 'heuweltjies'. 'Heuweltjies' are mounds rising to 1 m in height, generally circular in shape with diameters up to 30 m and presumably zoogenic in origin (Lovegrove & Siegfried 1986). They are similar to the Mima-like mounds covering extensive areas of western North America (Ross, Tester & Breckenridge 1968; Collins 1975; Cox 1984), the Peruvian altiplano (Scheffer 1958) and many altitudinal and climatic zones of Africa (Glover, Trump & Wateridge 1964; Cox & Gakahu 1983; Darlington 1985) with on-mound soils being more permeable to water, having lower bulk densities and higher levels of organic matter than off-mound soils. Midgley, G. F. & Musil, C. F. (unpublished) found for 'heuweltjies' in the Worcester region of the Cape Province, South Africa (roughly 250 km west-south-west of Tierberg) that on-mound soils are alkaline and rich in calcium with higher soil water contents and macro- and micro-elemental concentrations than

off-mound soils. These elements are concentrated in 'heuweltjies' due to changes in soil texture, in the distribution of organic matter, in the chemical properties of the soil and in the distribution of plant nutrients as a result of animal activities (Petal 1978; Wood & Sands 1978; Lovegrove & Siegfried 1986). They are primarily responsible for the 50% greater plant cover reported on 'heuweltjies' than on adjacent off-mound soils in the Worcester area (Midgley G. F. & Musil, C. F.; unpublished). Further plant turnover on 'heuweltjies' will continue to enrich the concentration of nutrients there. This process will proceed as long as animals utilize the 'heuweltjie'. Once animal activity ceases, surficial organic materials will no longer be relocated into the mound but rather will be lost through the effects of wind and water moving these materials off the mound.

We suggest that erosion affects the pH and chemical composition of the soils downslope from a 'heuweltjie' creating a small-scale environmental gradient. Eventually these soil chemical effects will diminish as animal activities cease on the 'heuweltjie'. We hypothesize that these more basic, calcium-rich soils favour species such as *Brownanthus* and *P. pallens* and that as these soils become more acidic, species such as *Eberlanzia* and other members of the woody shrub guild establish. Therefore, the driving forces in this plant community are the mechanisms by which Ca and other elements are concentrated in a 'heuweltjie' and the factors, including overgrazing, which lead to their erosion.

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References

Acocks, J. P. H. 1975. Veld types of South Africa. Mem. Bot. Survey S. Afr. 40: 1–128.

Bond, W. 1987. The Karoo biome project: early days. S. Afr. J. Sci. 83: 453–454.

Cody, M. L. 1978. Distribution ecology of *Happlopappus* and *Chrysothamnus* in the Mojave Desert. I. Niche position and niche shifts on north-facing granitic slopes. Amer. J. Bot. 65: 1107–1116.

Cody, M. L. 1986. Spacing patterns in Mojave Desert plant communities: near-neighbor analyses. J. Arid Envir. 11: 199–217.

Collins, B. 1975. Range vegetation and mima mounds in North Texas. J. Range Mgmt. 28: 209–211.

Cowling, R. M. 1986. Whither Karoo research? S. Afr. J. Sci. 82: 409–411.

Cox, G. W. 1984. The distribution and origin of Mima mound grasslands in San Diego County, California. Ecology 65: 1397–1405.

Cox, G. W. & Gakahu, C. G. 1983. Mima mounds in the Kenya highlands: significance for the Dalquest-Scheffer hypothesis. Oecologia (Berl.) 57: 170–174.

Darlington, J. E. P. C. 1985. Lenticular soil mounds in the Kenya highlands. Oecologia (Berl.) 66: 116–121.

Ellis, F. & Lambrechts, J. J. N. 1986. The Karoo biome: a preliminary synthesis. Part I – physical environment; soils. S. Afr. Nat. Sci. Prgm. Rep. 124: 18–38.

Fontyne, P. J. & Mahall, B. E. 1981. An experimental analysis of structure in a desert plant community. J. Ecol. 69: 883–896.

Glover, P. E., Trump, E. C. & Wateridge, L. E. D. 1964. Termitaria and vegetation patterns on the Loita Plains of Kenya. J. Ecol. 52: 367–377.

Grieg-Smith, P. 1983. Quantitative Plant Ecology. Blackwell Sci. Publ., Oxford.

Hoffman, M. T. & Cowling, R. M. 1987. The Karoo biome: a preliminary synthesis. Part II – vegetation and history; plant physiognomy, phenology and demography. S. Afr. Sci. Prgm. Rep. 142: 1–34.

Lovegrove, B. G. & Siegfried, W. R. 1986. Distribution and formation of Mima-type earth mounds in the western Cape Province of South Africa. S. Afr. J. Sci. 82: 432–436.

McAuliffe, J. R. 1988. Markovian dynamics of simple and complex desert plant communities. Amer. Natur. 131: 459–490.

Petal, J. 1978. The role of ants in ecosystems. In: Brian, M. V. (ed.), Production Ecology of Ants and Termites. pp. 293–325. Cambridge Univ. Press, Cambridge.

Phillips, D. L. & MacMahon, J. A. 1981. Competition and spacing patterns in desert shrubs. J. Ecol. 69: 97–115.

Pielou, E. C. 1960. A single mechanism to account for regular, random and aggregated populations. J. Ecol. 48: 575–584.

Ross, B. A., Tester, J. R. & Breckenridge, W. J. 1968.

Ecology of Mima-type mounds in northwestern Minnesota. Ecology 49: 172–177.

Roux, P. W. & Vorster, M. 1983. Development of veld management research in the Karoo region. Proc. Grassl. Soc. sth. Afr. 18: 30–34.

Rutherford, M. C. & Westfall, R. H. (1986). The biomes of southern Africa – an objective categorization. Mem. Bot. Surv. S. Afr. 54: 1–98.

Scheffer, V. B. 1958. Do fossorial rodents originate Mima-type microrelief? Amer. Midl. Natur. 59: 505–510.

Siegel, S. 1956. Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill, New York.

Vandermeer, J. 1980. Saguaros and nurse trees: A new hypothesis to account for population fluctuations. Southwestern Natur. 25: 357–360.

Vasek, F. C. 1979/1980. Early successional stages in Mojave Desert shrub vegetation. Israel J. Bot. 28: 133–148.

Vasek, F. C. & Lund, L. J. 1980. Soil characteristics associated with a primary plant succession on a Mojave Desert dry lake. Ecology 61: 1013–1018.

Venter, J. M., Mocke, C. & De Jager, J. M. 1986. The Karoo biome: a preliminary synthesis. Part I – physical environment; climate. S. Afr. Nat. Sci. Prgm. Rep. 124: 39–52.

Visser, J. N. J. 1986. The Karoo biome: a preliminary synthesis. Part I – physical environment; geology. S. Afr. Nat. Sci. Prgm. Rep. 124: 1–17.

Weather Bureau 1954. Climate of South Africa. The Government Printer, Pretoria.

Wood, T. G. & Sands, W. A. (1978). The role of termites in ecosystems. In: Brian, M. V. (ed.), Production Ecology of Ants and Termites. pp. 245–292. Cambridge Univ. Press, Cambridge.

Yeaton, R. I. 1978. A cyclical relationship between *Larrea tridentata* and *Opuntia leptocaulis* in the northern Chihuahuan desert. J. Ecol. 66: 651–656.

Yeaton, R. I. 1988. Structure and function of the Namib dune grasslands: characteristics of the environmental gradients and species distributions. J. Ecol. 76: 744–758.

Yeaton, R. I. 1990. Structure and function of the Namib dune grasslands: species interactions. J. Arid Envir. 18: 343–349

Yeaton, R. I. & Cody, M. L. 1976. Competition and spacing in plant communities: the northern Mohave Desert. J. Ecol. 64: 689–696.

Yeaton, R. I. & Cody, M. L. 1979. The distribution of cacti along environmental gradients in the Sonoran and Mohave deserts. J. Ecol. 67: 529–541.